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ORIGIN OF PRAIRIES IN ILLINOIS

CONTRIBUTIONS FROM THE HULL BOTANICAL LABORATORY **314**

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The prairie province, which extends from Texas into Canada, covers the western part of Minnesota, but farther south extends eastward across Iowa, Illinois, and southern Wisconsin into the western part of Indiana. ATWATER (**2**) described a few isolated areas of prairie in Ohio, but nearly all of Ohio, as well as the greater part of Indiana, was forested when it was first settled by white men. The prairies extend almost down to the Ozark Hills in Illinois and almost to the Missouri River in central Missouri. South of the Missouri River they extend a short distance into southwest Missouri, but farther south they do not reach the eastern boundary of either Oklahoma or Texas. Some areas of prairie are found along the Gulf Coast in Louisiana and farther north in Mississippi and Alabama.

In the study of any prairie region, it is necessary to determine the conditions at the time of the prairie's origin which favored the invasion of a grass rather than a tree vegetation. As most of the prairies had their origin thousands of years ago, one can readily see that it is not easy to recognize all the conditions that influenced the course of plant succession. It is not necessary to assume that all prairies originated under the same conditions; in fact, it seems certain that they did not. The same effect may be the result of causes which differed more or less. It is necessary also to consider the

conditions that have been in operation since the origin of the prairie. It does not necessarily hold that an area which has been occupied by prairie grasses will remain a prairie indefinitely. It is possible that the conditions in some places may not prevent the invasion of a prairie by forests, but may make the invasion very slow. Such places will remain as prairies for a much longer time than areas in which the conditions favor a more rapid invasion of prairie by forests. In a typical "grassland climate," such as is found in the main part of the prairie province, it is reasonable to suppose that the vegetation has reached a fairly static condition, and that there will be little change so long as the climate remains fairly constant. On the other hand, in Illinois, which is in a "woodland climate," it may be that the forests are invading the prairies, and that the prairies remain because the conditions prevent a rapid invasion, and the time since the origin of the prairies has been too brief for their complete occupation by forests.

Previous investigations have shown that prairies generally have a xerophytic vegetation; that the evaporation rate is much higher there than in adjoining forests, while the soil moisture content is much lower; and that, after the prairie is formed, it is difficult for tree seedlings to become established, except along forest borders and on eroded slopes. This paper reports an attempt to determine the conditions which favored the invasion of this region by grasses rather than by trees at the time the prairies were formed, and also attempts to determine the factors which have influenced the rate of invasion of forests into the prairies since their origin. "The actual cause of the treelessness of the prairies is not to be found in any of the present conditions" (GLEASON 15). Present conditions are important only as they help to interpret the past. A prairie is treeless because at the time of its origin the conditions favored the invasion of a grass rather than a tree vegetation, and the rate of forest invasion has been too slow for the complete occupation of the area by trees during the time which has elapsed since the prairie was formed. It is necessary to study present conditions, but it is also necessary to study past conditions. In this way only can one explain the present distribution of prairie and forest in Illinois and neighboring states.

The dominant prairie species are xerophytic grasses. This is shown by investigations of prairies in Illinois and in other parts of the world. The sand prairies along the Illinois River were studied by GLEASON (16) and VESTAL (41). Both investigators found xerophytic associations dominated by bunch grasses, among which were *Koeleria cristata*, *Leptoloma cognatum*, *Stipa spartea*, *Panicum pseudopubescens*, *Bouteloua hirsuta*, *B. curtipendula*, *Cyperus Schweinitzii*, *Andropogon scoparius*, and *A. furcatus*. VESTAL (40) studied a black soil prairie west of Chicago. He found two upland prairie grass associations, one dominated by *Andropogon scoparius* and the other by *A. furcatus*. The depressions were occupied by a marsh association, with *Liatris spicata*, *Eryngium yuccifolium*, *Spartina Michauxiana*, *Calamagrostis canadensis*, *Phragmites communis*, *Glyceria minata*, *Scirpus lineatus*, and *Typha latifolia*. SAMPSON (30) studied the prairie vegetation in all parts of Illinois:

> *Andropogon furcatus* is the climax grass of the whole upland prairie region of the state, and in the succession leading to this climax from the more xerophytic uplands and exposed clay soils *Andropogon scoparius* is the most important species.

According to SAMPSON, the sand prairie vegetation has a tendency to develop into the typical upland prairie vegetation with *Andropogon furcatus* as the dominant species, while the marsh grasses in the depressions are often replaced by *A. furcatus* when the depressions are drained.

In other parts of the prairie province, as well as in grassland regions in other parts of the world, the dominant plants are species of *Andropogon*, *Stipa*, or other xerophytic grasses. SCHAFFNER (31) lists *Andropogon furcatus* and *A. scoparius* as the two most important prairie grasses in Clay County, Kansas. HITCHCOCK (23) found *A. furcatus*, *A. scoparius*, and *Chrysopogon nutans* dominant on the prairies of eastern Kansas, while the more xerophytic *Buchloe dactyloides* was dominant in western Kansas. HARVEY (21) studied the prairie vegetation in southeastern South Dakota and found six dominant species: *Bouteloua oligostachya*, *B. curtipendula*, *B. hirsuta*, *Koeleria cristata*, *Andropogon furcatus*, and *A. scoparius*. SMITH (35) studied grazing conditions in the prairies

of western Texas. He said the original vegetation was "largely blue stems and sage grasses (*Andropogon*)," and that these had been killed out by overgrazing and their places taken by other xerophytic grasses which were less desirable for pasture. HARPER (**19**) studied the vegetation on some Alabama prairies, and found the most abundant species was *Andropogon scoparius*. POUND and CLEMENTS (**29**) list a number of xerophytic grasses as dominant species in the prairie province. SHIMEK (**33**) found prairie plants growing on sand dunes, and emphasized the fact that these plants are xerophytes and can exist on dunes "as well as on the xerophytic surfaces of ordinary prairie." KOSSOWITSCH (**24**) found the steppes of Russia covered with xerophytic grasses, the most important of which are species of *Stipa*. SCHIMPER (**32**) describes the savannah as a region with xerophilous vegetation, of which "the majority of individual plants are grasses."

Prairies occupy areas where the irregularities of the surface are too slight to check the velocity of the wind to any great extent. The desiccating action of strong winds, especially the dry southwest winds, is very great. It is not surprising, therefore, that prairies have a high evaporation rate with correspondingly low soil moisture content during the latter part of the growing season. GLEASON and GATES (**17**) studied evaporation rates in *Quercus velutina* woods and in several stations in the sand prairies of central Illinois. The evaporation from a standard atmometer, which was placed in open ground where there were only a few weeds, was taken as 1, and the evaporation at the other stations recorded as ratios of the number. The evaporation rates at the prairie stations varied from 1.04 to 1.56, while the rate at the forest station was only 0.66. HARVEY (**22**) studied evaporation and soil moisture in a prairie near Chicago. He found the mean daily rate for the season higher than in the pine dunes, but lower than in the cottonwood dunes along the south shore of Lake Michigan. During the summer the soil moisture was low, often falling below the wilting coefficient. In Nebraska similar studies were carried out by WEAVER and THIEL (**46**), and by POOL, WEAVER, and JEAN (**28**). In both investigations a much higher evaporation rate was found on the prairies than in adjoining forests. The soil moisture content was much lower in the prairie than in the

forest, falling below the wilting coefficient to a depth of two feet during part of the summer. WEAVER (45) found higher evaporation rates on southwestern slopes than on northeastern slopes in southeastern Washington. Some of the northeastern slopes were forested, while the southwestern slopes were treeless. In western Iowa, SHIMEK (33) observed similar relations between the evaporation rates and forest distribution. TODD (36) observed heavy timber on protected slopes, while there was little or none on exposed slopes in southwestern Iowa. VESTAL (43) found local inclusions of prairie within forest on slopes near the Embarrass River in the vicinity of Charleston, Illinois. These prairie areas are on the upper part of south-facing slopes where they are exposed to the desiccating effect of the southwest winds. HANSON (18) studied some prairie inclusions found in deciduous forests in Ohio, Illinois, Iowa, and eastern Nebraska. He found the evaporation rate much higher on the prairie than in the forests, while the soil moisture content was much lower in the prairies. In one of the forest stations the soil moisture content fell below the wilting coefficient once during the summer, but in the high prairie there was no water available for plants at four different times in the 0–10 cm. layer, and twice in the 10–30 cm. layer. Within forests evaporation is less in ravines than on the higher ground, as shown by TRANSEAU (37), FULLER (13), and ULLRICH (38). The evaporation rate seems to vary directly and the soil moisture content inversely with the wind velocity.

Tree seedlings have difficulty in becoming established on prairies because of the thick prairie sod and the desiccating action of the wind. Where artificial plantings are made, the trees grow and develop normally. Such an artificial planting in eastern Nebraska is described by POOL (27). In this grove the shade killed out the prairie grasses and they were replaced by mesophytic herbs. On the other hand, where forests have been destroyed by man, the mesophytic herbs die and xerophytic prairie grasses may replace them. SHIMEK (34) found a prairie vegetation along a road through a forest in Iowa. The destruction of the trees along the road exposed the mesophytic forest herbs to intense sunlight and strong winds, which killed them and allowed the invasion of the xerophytic grasses.

VESTAL (**42**) found a similar invasion of prairie grasses into a forest along the Big Four right of way near the Embarrass River in Illinois. Both of these areas would undoubtedly soon be reforested if man did not continually destroy the young tree growth. On the open prairie, however, the exposure is much greater, and prairie groves are rare. North of Charleston, in Coles County, Illinois, there is a small prairie grove which is on some low ridges at some distance from other timber. GATES (**14**) mentions isolated oaks on the body of the prairie, but thinks the invasion along forest borders, where the shade kills out the grasses, is much more important. SAMPSON (**30**) mentions four methods of invasion of prairies by forests:

> (1) Forest invasion accompanying erosion by streams, (2) growth of tree seedlings along forest borders where the grasses are checked by the shade of overhanging branches, (3) the occasional establishment of isolated seedlings farther out on the prairie, and (4) the growth of adventitious branch buds from the roots of certain trees and shrubs extending short distances into the prairie.

In western Texas, BRAY (**5**) found chaparral invading the prairie where the grass sod was destroyed by overgrazing. WELLS (**47**) reported forests on areas around St. Louis that were prairie when first settled by white men.

It is evident that prairies have a xerophytic vegetation because the wind velocity and evaporation rate are high while the soil moisture is low during the latter part of the growing season. Xerophytic grasses are able to make a rapid growth while there is sufficient water in the soil. They store food in their underground parts and go into a dormant condition during the dry weather. Tree seedlings are unable to compete with the grasses on the open prairie, but along the slopes of gullies and streams and some of the steeper moraines erosion removes the grass sod, and the irregularities of the surface check the wind velocity and reduce the evaporation, so that tree seedlings are able to secure a foothold. Trees can also advance slowly out on the prairie along the forest borders where shade kills out the grasses and the forest checks the wind velocity. The latter is very slow, so that the rate of advance depends to a large extent on the topography. It is necessary, therefore, to study the physiographic conditions in Illinois and neighboring states, for the differences in physiography are important in determining the present distribution of the prairies.

The Illinois prairies are postglacial in origin. According to CHAMBERLIN and SALISBURY (**6**), there were six different periods of glacial ice advance, which were separated by periods when the land was free from ice. The period between the Early and Late Wisconsin ice advances was relatively short, but all the other interglacial periods were very long. As each ice sheet advanced, it modified the surface of the country. As a general rule, the hills were leveled and the valleys filled, but in some places steep morainal ridges were formed by the glaciers. In this region, the surface left by the earliest glacier has been completely overrun by later ice advances, but all the other ice sheets left large areas where the surface has not been modified by later glacial advances. The Kansan ice sheet invaded northeastern Kansas and entered Missouri, extending as far south as the Missouri River. The Illinoisan ice sheet only entered the eastern edge of Iowa, but covered the greater part of Illinois, extending down to the Ozark Hills in the southern part of the state. Just east of the Illinois-Indiana line the border of the Illinois drift bends to the northeast, follows this direction to central Indiana, then turns south to the Ohio River, then east to south central Ohio, and then north to central Ohio, where it is buried by drift of the Wisconsin ice sheets. The Iowan ice covered northeastern Iowa and possibly a small area in northwestern Illinois. The Early Wisconsin glacier entered northeastern Illinois and extended as far south as Shelbyville and Mattoon, but in Indiana and western Ohio it extended almost to the border of the Illinoisan drift. A lobe of the Late Wisconsin ice sheet entered western Iowa, extending as far south as Des Moines. Another lobe entered northeastern Illinois, but did not extend as far to the west or south as the Early Wisconsin. Farther east, however, it covered nearly all of the Early Wisconsin drift in Indiana and western Ohio, and overrode all earlier drift sheets in eastern Ohio.

The glaciated region is bordered on the south by rough, hilly country from eastern Ohio to the western slopes of the Ozark Mountains in Missouri. Farther west, in the plains region, the relief is moderate. The Late Wisconsin drift has a very uneven surface, with many morainal ridges and depressions, but the Early Wisconsin, although it has some strong moraines, is nearly level over large areas in east central Illinois. The earlier drift sheets were originally

nearly plane, but there must have been considerable pre-Wisconsin erosion near the larger streams, such as the Missouri, Mississippi, Rock, and Illinois Rivers. Much of the area, however, is still nearly level, as it was when the glaciers retreated. During the retreat of the last ice sheet a large lake, Lake Chicago, was formed in the southern end of the Lake Michigan basin, and another one, Lake Maumee, in the western end of the Lake Erie basin. Drainage to the north and east was blocked by the glacial ice, so that both of these lakes found outlets to the southwest, the former through the Chicago outlet and the Des Plaines River to the Illinois River, and the latter through the Wabash Valley to the Ohio River.

At the present time, large ice fields are bordered by treeless wastes, called tundras, where the vegetation is mainly mosses and lichens. The tundra varies in width in different regions and is often bordered on the south by forests. WARMING (**44**) says the tundra occupies only small areas in mountainous countries like Greenland, while it is very extensive in flat countries like northern Siberia. During the ice age conditions along the border of the ice fields must have been similar to those in Greenland and northern Siberia at the present time. The forest zone must have been separated from the ice front by a tundra zone which was narrow where the country was rough and hilly, but very wide where the country was comparatively level. During each ice advance, the tree line was depressed and the forests were "replaced by scrub, bog, and tundra" (CLEMENTS **7**). Where the country was flat, the tree line was undoubtedly depressed for a great distance below the ice front, but where the country was rough and hilly, it is probable that, as pointed out by HARSHBERGER (**20**), "the glaciers did not affect the tree distribution at any great distance from the ice front." At the time of the maximum advance of the Late Wisconsin ice sheet, it is probable that trees were found only a short distance from the ice front in eastern Ohio, where the country is rough and hilly. In southwestern Ohio and southern Indiana the country is hilly, but it is not so rough as in eastern Ohio, so that the tundra zone was probably somewhat wider but still comparatively narrow. Farther west, however, where there was a wide belt of comparatively level country below the ice front, the tundra must have covered all the country as

far south as the Ozark Hills in Illinois and the dissected bluffs along the Missouri River in Missouri, except the "driftless area" in northwestern Illinois and southwestern Wisconsin, and possibly some protected slopes along the larger streams such as the Mississippi, Rock, and Illinois Rivers.

Below the tundra, the rough, hilly country between the Appalachian Mountains and the west slopes of the Ozark Mountains was undoubtedly forested. Near the tundra the forests probably included both conifers and hardwoods, with the conifers on the exposed slopes and hilltops and the hardwoods along the protected slopes. In the plains region there were probably some protected slopes along some of the streams where trees were able to grow, and there may have been some depressions which were occupied by willows and tamaracks. As the greater part of the surface is gently rolling, however, tree seedlings would have been killed by the desiccating action of the strong winds. It is probable that the region as a whole was treeless, and that prairies bordered the tundra. At the time of the maximum advance of the Late Wisconsin ice sheet it is probable that the tundra, which was the first vegetation zone below the glacier, was narrow in Ohio and Indiana but very wide in the flat country farther west, extending almost to the southern end of Illinois and almost to the Missouri River in Missouri. South of the tundra there were undoubtedly forests extending from eastern Ohio to Missouri, while the country farther west was probably treeless plains covered by prairie grasses.

When the Late Wisconsin glacier began its retreat, it left a bare area that was invaded by the mosses and lichens of the tundra. These plants can endure the severe climatic conditions along the ice front, and can live on the pulverized rock material left by the glacier. Other plants were excluded by the severe climate and the inhospitable soil. As the ice retreated farther to the north the climate became less severe, and the tundra plants gradually added organic matter to the substratum and developed a soil suitable for the growth of the higher plants. According to ADAMS (1) the tundra was invaded by coniferous forests, and these by deciduous forests in the southeast and arid plains vegetation in the southwest. The actual condition, however, was not so simple as this. As

already mentioned, it is doubtful whether there was any conifer belt along the tundra in the plains region. In this region, therefore, the prairie merged gradually into the tundra, and the latter must have been invaded by grasses from the former. Farther east, where forests joined the tundra on the south, both conifers and hardwoods moved northward, but their invasion was restricted to stream valleys and slopes, and to that part of the till sheet where there were considerable irregularities in the surface. On the level to gently rolling country, where there was no protection from the desiccating action of the strong winds, tree seedlings could not become established, and these areas must have been occupied by grasses. It seems probable that the prairie grasses, which invaded the tundra in the plains region, moved eastward, occupying all the country from which trees were excluded.

There may have been a postglacial period of aridity, but it is not necessary to assume such a condition in order to explain the origin of the prairies. Under the present moisture conditions, movement of forests into flat country is extremely slow. If the moisture conditions during all the years since the ice age were similar to what they are now, the northward movement of trees was very slow. If there was an arid postglacial period, the advance of the forests during that period was delayed, and may have been entirely prevented for a time, but it was resumed again when the climate became more moist. In either case, most of Illinois and Iowa, and large areas in northern Missouri, northern Indiana, and western Ohio must have developed from tundra into prairie. If there was an arid postglacial period, there may have been no invasion of the prairies by forests until the close of this arid period, but, if there was no such period, forest invasion began immediately, and has been going on slowly but steadily ever since the close of the ice age. The rate of invasion varies with the topography, and explains why some areas are completely forested while others are treeless prairies.

During the ice age the tundra, which covered most of Illinois and large areas in neighboring states, must have been similar to that found in the region west of Hudson Bay at the present time. HARSHBERGER (**20**) describes this region as follows:

> It is a treeless wilderness, low and marshy, interspersed with lakes, streams, and mossy plains, the so-called arctic tundra. The soil is permanently frozen

to a great depth, and in summer it thaws out a foot or two to permit the grasses, sedges, and other plants of the region to make a rapid vegetative growth.

Similar conditions probably prevailed in the tundra along the ice front during the Late Wisconsin glaciation. As the ice sheet retreated farther to the north, the summers gradually lengthened and the soil thawed to a greater depth. This permitted drainage of the higher ground, which was then invaded by the more xerophytic grasses, while the swamp grasses and sedges, which were the pioneer invaders of the tundra, were restricted to the depressions, which remained wet all summer. The invasion of the prairie grasses was probably rapid, and it seems likely that, early in post-glacial times, an immense prairie, with xerophytic grasses on the higher ground and swamp grasses in the depressions, had replaced most of the tundra in Iowa, Missouri, Illinois, Indiana, and Ohio. The grasses which grew on this prairie may have included the same species found on prairies today, and *Andropogon furcatus* may have been the dominant species as it is now on the prairies of Illinois.

As previously mentioned, the Late Wisconsin drift has an irregular surface with many morainal hills and depressions. When the ice retreated, the part of this drift sheet which is in Ohio and Indiana was separated from the forests on the south by a narrow strip of treeless tundra, while, farther west, there was a wide area of earlier drift which was nearly level and treeless. In this older drift, however, there were some large pre-Wisconsin stream valleys, such as the Mississippi, Rock, Illinois, and Wabash Rivers. The drainage waters from the glacial lakes for a time emptied into the Illinois and Wabash Rivers, and rapidly extended the valleys of these streams into the Late Wisconsin drift. These stream valleys were avenues for the rapid advance of forests.

This region was invaded by two types of forest vegetation, the upland and the bottomland. The latter followed the stream valleys, while the former advanced along the bluffs of the larger streams and in other places where the topography was rough. The upland pioneers were the pines, which early entered the rough country in northeastern Ohio and passed on into the morainal region of Ontario, where some of their descendants are still found. Conifers must have advanced rapidly along the Wabash, Illinois, Rock, and Mississippi Rivers. There are still white pine forests along the Rock

River which DE FOREST (12) thinks are relics of former more extensive pine forests. COWLES (10) mentions forests along the Illinois River at Starved Rock, where "the dominant tree vegetation is coniferous, consisting especially of the white pine (*Pinus Strobus*), and the arbor vitae (*Thuja occidentalis*)." As the pines are wind disseminated, it is probable that they advanced rapidly along these stream bluffs and spread rapidly in the rougher morainal regions of the Late Wisconsin drift. The pines were followed probably by the oaks, and these in some places by maples and beeches. In some places along the stream bluffs xerophytic shrubs instead of pines may have preceded the oaks.

Along the river bottoms the invading trees were probably the same species as found in similar situations today. COWLES (11) studied the vegetation along the Des Plaines River, where the pioneer trees are *Salix nigra* and *S. longifolia*. These are followed by *Acer dasycarpum*, *Populus monilifera*, and *Fraxinus americana*. When the bottomland becomes drier, *Ulmus americana*, *U. fulva*, *Tilia americana*, *Juglans nigra*, and *J. cinerea* appear. These or similar species must have moved north along the stream valleys at the close of the ice age. In the tundra region below the drift deposited by the Late Wisconsin ice sheet, there were stream valleys where invasion was rapid. In the Late Wisconsin drift, however, invasion of the bottomland vegetation must have been determined by the rate of stream erosion, except where there were depressions that were invaded by these trees. As the seeds of most of these species are wind disseminated, they are easily scattered, and it seems likely that seeds from trees growing along streams that were cutting back into the fresh till would fall along the shores of small lakes and ponds in some of the depressions. Seeds falling along these shores would undoubtedly germinate and in turn scatter their seeds to other depressions. As there were many of these depressions in the Late Wisconsin drift, it seems likely that they were an important factor in hastening the invasion of this drift by forests. Some of the depressions, which remained continually wet because they were deep or fed by springs, developed into bogs. These bogs have been invaded by trees, and some of them entirely, but others only partially, occupied by forests.

Trees not only invaded the bottomlands and river bluffs, but they also moved up over the crest of the bluff and slowly moved out on the prairie. This invasion, as already noted, is very slow. In this invasion of the prairies it is probable that the oaks were pioneers, or xerophytic shrubs were the pioneers followed by the oaks. Where the bluffs are not dissected by tributary streams and gullies, the forest advance has been extremely slow, and there is only a very narrow belt of timber along the bluff. Where there has been considerable erosion, however, the forest belts are much wider. Where the gullies are close together, forests have often occupied the intervening area, but in some places narrow strips of prairie are still found along the tops of the ridges between the gullies. Where erosion has cut deep ravines, the vegetation quickly reaches the mesophytic forest stage. Near Charleston, Illinois, where the Embarrass River cuts through the Shelbyville moraine, there are many deep ravines which have an almost pure stand of *Acer saccharum*. Similar mesophytic conditions in ravines in the Chicago region have been described by COWLES (11). Where streams cut through moraines, trees not only occupy the slopes along the gullies, but they extend out along the slopes of the moraines beyond the heads of the gullies. This has been observed along the Shelbyville moraine near the Embarrass and Kaskaskia Rivers. In some places, especially along streams that are cutting back into flat prairies, erosion is not very deep, and the gullies extend only a short distance from the streams. These gullies are xerophytic, and it is probable that they were first invaded by xerophytic shrubs followed by oaks.

During the ice age the level uplands for a long distance below the ice front must have been free from tree vegetation. Trees, however, could grow along some of the stream bluffs and bottomlands. As the evaporation was less during the cold glacial period than during the warmer postglacial period, trees may have invaded stream valleys in the plains region from which they are now excluded. BESSEY (3) describes a deep canyon in western Nebraska where he found *Pinus ponderosa* var. *scopulorum*, *Juglans nigra*, and *Ostrya virginica*. These trees may be relics of vegetation which extended all along the streams during the glacial period, but was

unable to endure the greater postglacial evaporation in the more exposed situations.

As already mentioned, after the retreat of the last ice sheet trees moved northward, along the stream valleys, the shores of lakes and ponds, and the steeper morainal and preglacial ridges. After these areas were occupied, the trees slowly invaded the more level intervening areas. Where these intervening areas were small, they have been mainly or entirely occupied by the forests, but where they are large, a considerable part of them is still treeless. In eastern Ohio, where there are some preglacial ridges and many strong moraines, all the country was forested except a few bogs, which were only partially timbered, like the one in Trumbull County. A large part of western Ohio is comparatively level, but in this region the soil map of Ohio by COFFEY and RICE (**9**) shows many areas of soils that developed in timbered swamps. Large areas of these soils are found in the bed of glacial Lake Maumee and in the level areas between the larger streams. Smaller areas are scattered all over the till plain in western Ohio, and there are undoubtedly more which were too small to be shown on the map. If, as seems probable, these depressions were invaded by trees in early postglacial times, it is not surprising that the intervening areas have been occupied by forests except for a few comparatively small areas like those mentioned by ATWATER (**2**). In eastern Indiana the conditions are similar to those in western Ohio, but in western Indiana there is more flat country, and consequently a large area of prairie. This Indiana prairie is continuous with the Illinois prairies, as shown by COFFEY (**8**), who separated the soils in this region into dark colored prairie soils and light colored timbered soils.

In western Indiana, Illinois, Iowa, and northern Missouri, pre-Wisconsin erosion had dissected some of the country along the Wabash, Illinois, Rock, Mississippi, and Missouri Rivers. Between these streams the country south of the Late Wisconsin drift is comparatively level. These flat areas have few depressions, so that the invasion of forests has been almost entirely along streams and gullies, and the slow advance along the forest border. In southern Illinois forests extended farther out into the flat prairies than they did in central and northwestern Illinois, because invasion began

much sooner in southern Illinois than farther north. In northeastern Illinois, however, where the Late Wisconsin glacier left an uneven surface, forests have advanced out on many of the moraines between the streams, although the time has been much shorter. During the Late Wisconsin glaciation the tundra probably extended to the rough country in southern and eastern Williamson County, Illinois. The flat country in the central and northwestern parts of this county must have had a tundra vegetation which was later invaded by the prairie, a few small remnants of which still remain as prairie. In Franklin and Perry Counties more of the inter-stream areas is still prairie, while in Champaign County the forests occupy only narrow strips along the streams. Along some streams there are isolated areas of forests where the bluffs are eroded, while the gentle slopes are treeless. Low stream banks are often treeless for long distances, but steep bluffs are almost always timbered. These differences have been observed in different parts of Illinois, and similar differences in other parts of the state have been shown by the work of the Illinois Soil Survey (**39**).

MOSIER early recognized the differences between the prairie and forest soils, and in his classification the soils are grouped into prairie and timbered soils. These differences make it possible to map the boundary between forest and prairie in places where the forests have been cleared and both forest and prairie are now under cultivation. The Illinois soil maps, therefore, show the location of prairie and forest, and when the work is completed, they will show the distribution of prairie and forest in all parts of the state. COFFEY'S (**8**) map is valuable in showing the distribution of prairie and forest in the United States as a whole, but he grouped the gray prairie soils of southern Illinois with the timbered soils because he considered the color more important, from the soil standpoint, than the vegetation. His map, therefore, does not show all the prairies in Illinois. As topography is an important factor in the classification of the timbered soils in Illinois, the maps give considerable information on the topography of the forested areas. The yellow silt loams and the yellow sandy loams occupy rough eroded areas. They are found on morainal and preglacial ridges where the slopes are steep, on bluffs, and in areas that are badly gullied. In some

places these eroded soils are found in narrow strips along bluffs, and in narrow tongues along gullies extending back into other timbered soils or even into the prairies. In other areas these soils occupy broad belts with jagged edges. The points along the jagged border are the heads of gullies that are separated by narrow steep ridges. The yellow gray silt loams and the yellow gray sandy loams vary in topography from slightly less rough than the eroded soils to almost level. They are found in areas of varying width bordering the eroded soils, along streams where the bluffs are low and the slopes too gentle for rapid erosion, and on moraines and preglacial ridges with gentle slopes. Flat or nearly level areas with an impervious clay subsoil are mapped as light gray silt loam on tight clay, white silt loam on tight clay, or yellow gray silt loam on tight clay. These soils are found mainly in the southern part of the state, and represent areas that were formerly prairie soils, either gray silt loam on tight clay or brown gray silt loam on tight clay. The timber (mainly oaks) has changed the character of the soil, particularly the color of the surface soil, which is a lighter gray than in the prairie soils from which they were derived. The soil maps of Bond and Clay Counties show that a large part of these soils is between streams and gullies where the invading trees advanced from opposite directions. Some of the light gray silt loam on tight clay in these counties is along the edge of the prairies, and shows that the trees have been able to invade the flat prairie for some distance. As these areas are in the southern part of the state and are near the Wabash and Kaskaskia Rivers, the time for this invasion must have been very long. In these counties there are some small timbered ridges surrounded by prairie and some areas of prairie surrounded by timber. Farther north, in Moultrie County, where there is less erosion and the forest invasion began at a much later date, the forests extended only a short distance from the streams. Adams County, which lies between the Mississippi and Illinois Rivers, is badly dissected, and the greater part is timbered. Many narrow strips of prairie are found on the tops of ridges between the streams and gullies. In Lake, Kane, and DuPage Counties, which are in the Late Wisconsin glaciation, a large part of the irregular surface is forested.

All the evidence indicates a once more extensive prairie region in Illinois and the neighboring states, which has gradually been reduced in area by the invasion of trees. Fires probably have retarded the advance of the forests, but they are not responsible for the treelessness of the prairies (BOURNE **4**). Where forests have been destroyed locally by fires, it is doubtful whether the area is ever occupied by prairie grasses. Such areas are generally invaded by fire weeds followed by brambles and then trees. The idea of LESQUEREUX (**25**), that "all the prairies of the Mississippi valley have been formed by the slow recess of sheets of water of various extent, first transformed into swamps and by and by drained and dried," is also untenable. MCGUIRE (**26**) suggested that the Alabama prairies once constituted the boundary of the Atlantic Ocean, and it may be that these prairies, as well as some others in unglaciated regions, are relics of the grass vegetation which first invaded the bare area left by the withdrawal of the oceanic waters. The prairies of Illinois and neighboring states, however, are in a region that was covered by glacial ice during the Pleistocene Period. At one time geologists believed the loess was a water deposit. If such had been the case, it would be reasonable to suppose that the prairies arose on the recession of the waters that deposited the loess. There is no evidence, however, that all, or even a large part of Illinois and the neighboring states was ever covered by water since the ice age. The loess is now believed to be wind deposited, and the prairies found on these loess deposits could hardly have arisen from swamps that were formed on the recession of water. During the ice age, there must have been a tundra along the border of the ice, just as there is along the borders of ice sheets at the present time. It seems likely that this tundra covered all of Illinois where prairies are now found, and that the tundra was invaded by prairie grasses when the glacier receded. As postglacial time has been too short for the complete occupation of this region by forests, part of Illinois is still prairie, but it is probable that all of Illinois would eventually have been forested, if man had not put a stop to all natural succession. The rate of invasion of flat prairies is very slow, however, and it would take a very long time for the forests to completely occupy these areas.

Summary

1. The prairies of Illinois are near the eastern edge of an eastern extension of the prairie province, and are really in a region with a "woodland climate."

2. Previous investigations have shown that prairies generally have a xerophytic vegetation, a high evaporation rate, and a low soil moisture content during part of the growing season; and that tree seedlings are generally excluded from the body of the prairie, but are able to invade the prairie slowly along the borders of forests and more rapidly along streams and ridge slopes.

3. Most of Illinois is covered by glacial drift which was deposited during several ice advances. The earlier glacial deposits, which cover most of the glaciated area in Illinois, were originally comparatively level, while the last drift sheet, which entered northeastern Illinois and covered most of the states to the north and east, has an irregular surface with many moraines and depressions. Part of the earlier drift was eroded by large streams before the advance of the last ice sheet. The glacial lakes, Chicago and Maumee, excavated outlet channels through the last drift sheet.

4. During the ice age there must have been a tundra along the border of the ice, just as there is in the Arctic regions at the present time. This tundra was probaby narrow in Ohio and Indiana, but very wide in the level country farther west, extending nearly to the southern end of Illinois and nearly to the Missouri River in Missouri. South of the tundra there were undoubtedly forests in the rough country, which extended from Ohio to Missouri, but treeless prairies in the level plains region farther west.

5. When the last ice sheet retreated, the bare area which it left was invaded by the tundra, and the tundra was invaded by other plants. In the plains region prairie grasses invaded the adjoining tundra, and moved east, occupying all the level country, from which trees were excluded by the desiccating action of the strong winds. It is probable that all the level country as far east as Ohio became prairie early in postglacial times. Forests invaded the hilly uplands and also along the stream valleys, and then spread to the shores of small lakes. After the forests occupied these areas they gradually moved out into the intervening areas.

6. In Ohio and eastern Indiana morainal hills and depressions are numerous and the intervening areas comparatively small, so that only a few small prairies remain in this region. Farther west, however, in western Indiana and Illinois, the flat inter-stream areas are larger, and many of them still remain as prairies, although forest trees have moved north along the larger stream valleys into the rougher country of Michigan and Wisconsin, which were almost completely forested.

7. The Illinois soil classification groups the soil types into prairie and timbered types, so that the soil maps of this state show the distribution of prairie and forest and the relation between stream dissection and forest invasion. The published maps show some invasion of moraines by the forests in northeastern Illinois, but in other parts of the state forest invasion has been confined almost exclusively to the slopes of streams and gullies and some of the adjoining level land.

8. Fires may have checked the invasion of forests into prairies, but prairies never originated by the destruction of forests by fires. Some unglaciated regions may have prairies that are relics of the vegetation that invaded the land when it first appeared above sea level, but the Illinois prairies are in a glaciated region, and there is no evidence that this region was covered by water at any time since the ice age. During the glacial period the prairie region of Illinois and neighboring states was probably occupied by a tundra which was invaded by prairie grasses. The prairie has been invaded by forests, and most of the states to the east and north of Illinois have been forested, but large areas in Illinois are still prairie, because post-glacial time has been too short for the forests to invade such large areas of level land.

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TEMPERATURE COEFFICIENT OF ABSORPTION IN SEEDS OF CORN

CONTRIBUTIONS FROM THE HULL BOTANICAL LABORATORY 315

CHARLES A. SHULL AND S. P. SHULL

(WITH ONE FIGURE)

Introduction

In a previous paper (17) dealing with the temperature coefficient of moisture absorption in seeds, it was shown that the curves of water intake for cocklebur seeds and for cotyledons of peas removed from their coats could be represented by one or a series of logarithmic equations having the general formula $y=a \log (bx+1)+c$. In this equation, y is the total intake at any moment, x is the time during which absorption has proceeded, and a, b, and c are constants. The velocity of water intake may then be represented by the formula $v=ae^{-k\phi}$, in which ϕ is the previous absorption. The velocity of water intake is therefore not an exponential function of the temperature, but an inverse exponential function of the amount of water previously absorbed. The value of the temperature coefficient, Q_{10}, varied in different tests from 1.55 to 1.83, values too low to support the theory that the rate of water absorption depends solely upon a chemical phenomenon, such as the simplification of associated water molecules as the temperature rises. Since it was found that the temperature coefficient was about the same whether or not a semipermeable membrane was present, it appears that semipermeability per se may not be an important factor in determining the rate of permeation of water through such membranes.

The original work on temperature and absorption was done by BROWN and WORLEY (6) on *Hordeum* seeds. Since none of the seeds used in the previous work belonged to the same family of plants as barley, and represented fatty and protein seeds rather than carbohydrate-high seeds, it was felt that the study should be continued with some member of the Gramineae. After several kinds were tested, corn was chosen because of certain obvious

advantages which it possesses. It has a tough coat, not easily ruptured, the coat can be removed readily, and is suited to certain membrane studies which are in progress. No other common member of the family offers such favorable material for direct permeability investigations.

Some preliminary experiments on corn were made by students at the University of Kansas, beginning in 1914. During the summer of that year BUSHNELL studied the influence of temperature and salts on the rate of water absorption in Leaming yellow dent corn, and was able to show indirectly that corn grains have osmotically active coats. It was apparent from the data, however, that the caryopsis coat is not as efficient in excluding NaCl and LiCl from the interior of the seed as is the seed coat of *Xanthium*. Before undertaking the collection of the data to be presented later, an attempt was made to analyze the data collected by BUSHNELL. Irregularities undoubtedly beyond the control of the investigator made the data useless for our purposes, and new series covering the range of BUSHNELL'S work were run with the greatest care.

A little later LOVEJOY removed the membrane from corn grains and used it in an osmometer similar to the one used by SHULL (16), and was able to confirm by direct measurements the indirect findings of BUSHNELL. The coats gave very good osmotic action, but were not entirely impermeable to the solutes used.

The temperature studies were resumed at the University of Kentucky, and have been concluded in the Hull Botanical Laboratory of the University of Chicago.

Materials and methods

In the later work, a variety of corn known as Hickory King has been used. It is a white dent corn with broad shallow grains and fairly hard endosperm. The breadth of the grains gives an excellent membrane for permeability studies. Attention has not been confined to this material, however, for even a casual survey of absorption phenomena shows that each individual kind of substance has its own peculiar water absorption complex. The physical structure or chemical composition of a material may so affect its water relations during absorption that mathematical treatment of

the data is precluded. In some cases the intake of water, as determined by successive weighings, is not so much a measure of the absorption of water as it is the measure of some other physical or chemical process. To illustrate these irregularities of absorption, a variety of substances has been used, including seeds, cherry wood blocks, and tissue from *Auricularia auricula-judae*, one of the Protobasidiomycetes whose gelatinous body is admirably adapted to such studies. Some of these irregular cases will be considered in connection with the general discussion, without attempt to present the heterogeneous data, which are not needed for a general understanding of the situation.

The methods of securing data, and of analyzing them, are the same as those used in a former study (**17**). Every possible precaution was taken to produce and maintain uniform conditions during the time periods of intake, and to reduce the inherent errors to a minimum. The value of taking such precautions is seen in the uniformity of the main intake curves. The data for analysis were selected from a large series of determinations, the selection being based on the absence of visible internal cracking or other evidence of abnormal behavior, and without any attempt to study the data mathematically before selection. It was felt that this kind of selection was justifiable, for when some sharp internal physical disarrangement of the seed occurs, such as cracking of the endosperm, the series in which it occurs is so irregular that it offers insuperable difficulties to the mathematical treatment.

As absorption in corn is much slower than in some other types of seeds, and the seed is so large that saturation is a matter of many hours, no attempt was made to carry the curves farther than 20 per cent intake. This affords six tangent measurements, each 2.5 per cent apart, running from 7.5 to 20 per cent, a sufficient number to give satisfactory values for Q_{10}, the coefficient for a 10° rise, over the range of these experiments. In order to lessen the labor involved in the analyses, the curves have not been run through the point of origin, but start at some point below 7.5 per cent of intake. The temperature range covered is much wider than in the earlier work, and provides a crucial test of the theory that absorption is dominated as to rate by a chemical process. Beginning at 5° C.,

data are presented for each 10° interval up to 55° C., a range wide enough for all practical purposes.

Experimental results

Only the data which have been used in the mathematical analyses need to be recorded here, one series for each temperature. The percentage of intake, with time, for six different temperatures, is shown in table I. The calculations are all based on the air dry weight of the seeds. The graphic presentation of the data is shown in fig. 1, from which the effects of temperature on absorption rates can be seen at a glance. The curves are all fairly regular, except the curve for 15° C., which for some reason runs low in the early part of the curve, and somewhat high in the later portion. This irregular formation for this curve modifies the ratios of absorption rates for the curves immediately above and below. This situation will be referred to in the presentation of the mathematical analysis of the data, which follows.

TABLE I

ABSORPTION OF WATER BY CORN IN PERCENTAGE OF AIR DRY WEIGHT

Time in minutes	Temperature					
	5°	15°	25°	35°	45°	55°
1	1.58	1.46	2.04	1.89	2.01	2.12
5	3.29	3.17	3.58	3.81	3.79	4.16
10	4.06	3.86	4.58	4.94	4.86	5.80
15	4.56	4.34	4.96	5.76	6.04	6.92
30	5.23	5.27	6.04	7.10	7.95	9.46
45	5.79	5.99	6.97	8.34	9.53	11.40
60	6.40	6.69	7.78	9.31	11.12	13.18
90	7.24	7.50	9.09	11.09	13.20	16.30
120	7.92	8.20	10.36	12.85	15.38	18.75
180	9.23	9.81	12.70	15.67	18.99	23.21
240	10.25	11.33	14.40	17.95	21.99	.....
300	11.26	12.89	16.06	19.87	24.24	.....
420	13.10	15.76	19.15	23.21	27.80	.....
540	14.55	17.83	21.67	.....	.....	.....
660	16.03	19.75	.....	.....	.....	.....
780	17.35	.....	.....	.....	.....	.....

Mathematical analysis

The rate of moisture intake at any given moment can be calculated very accurately from the tangent of the absorption curve at the time chosen. The tangent itself, however, cannot be measured

very accurately from an ordinary graph. In order to measure the velocity of absorption with accuracy, it was first necessary to construct mathematical curves of known form, which would follow the empirical data of table I as closely as possible. Then points of equal intake were chosen on each temperature curve, the tangents calculated from the formula, and the velocity of intake computed from the tangents.

The equation mentioned in the introduction serves admirably for the construction of these mathematical curves through the corn data, although it was developed in connection with the work on cockleburs and pea cotyledons. Indeed, one seldom finds biological data that approach the mathematical accuracy shown by these

TABLE II

FORMULAS OF CALCULATED CURVES

Temperature	Formula
5	$y=29.7 \log_{10}(0.0020x+1)+5.19$
15	$y=60.4 \log_{10}(0.0012x+1)+4.75$
25	$y=29.6 \log_{10}(0.0051x+1)+4.28$
35	$y=29.6 \log_{10}(0.0078x+1)+4.38$
45	$y=22.5 \log_{10}(0.0106x+1)+4.00$
55	$y=34.5 \log_{10}(0.0140x+1)+4.06$

water absorption curves for corn. By confining attention to the main curve of intake (omitting initial intake, and stopping before saturation effects were manifest), it has been possible to express each temperature curve by a single equation. It is quite probable that the initial intake curve and the approaching saturation curve could be followed by the same type of curve, with different constants, and with common tangents at the junction points of the curves. The procedure is tedious, however, and the analysis would add little to the interpretation of the process of absorption. This phase of the problem was adequately considered in the paper cited. The six equations for the six temperatures used, with numerical values substituted for the constants a, b, and c, are shown in table II.

The abnormality of the 15° curve mentioned in connection with the data is seen here, in the constants which were required to match the empirical data. Its disagreement with the other members of the family of curves will be seen more clearly in the intake ratios.

The extreme closeness with which the curves calculated from these six equations follow the experimental data of table I is shown in table III, where the calculated percentage of intake is given for each time interval; the amount of disagreement with the actual data is indicated, with a plus or minus sign to show whether the data are above or below the calculated intake. The columns indicating the discrepancy between the calculated intake of water and the actual intake observed are worthy of note. The largest difference between the theoretical and observed absorption is less than one-half per cent, and the average difference is only one-tenth of one per cent. Such close agreement is very remarkable for biological data.

TABLE III

INTAKE CALCULATED FROM FORMULAS, WITH DISCREPANCY OF DATA

TIME IN MINUTES	TEMPERATURE											
	5°		15°		25°		35°		45°		55°	
	Calculated	Data	Calculated	Data	Calculated	Data	Calculated	Data	Calculated	Data	Calculated	Data
10	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	6.02	−0.22
15	.....	.....	.....	.....	5.23	−0.27	5.80	−0.04	6.08	−0.04	6.92	0.00
30	.....	.....	5.68	−0.41	6.11	−0.07	7.08	+0.02	7.90	+0.05	9.31	+0.15
45	.....	.....	6.13	−0.14	6.94	+0.03	8.25	+0.09	9.50	+0.03	11.38	+0.02
60	6.65	−0.25	6.57	+0.12	7.71	+0.07	9.32	−0.01	10.95	+0.17	13.20	−0.02
90	7.32	−0.08	7.44	+0.06	9.13	−0.04	11.22	−0.13	13.46	−0.20	16.28	+0.02
120	7.96	−0.04	8.28	−0.02	10.42	−0.06	12.87	−0.02	15.58	−0.20	18.83	−0.08
180	9.16	+0.07	9.88	−0.07	12.65	+0.05	15.66	+0.01	19.07	−0.08	22.93	+0.28
240	10.25	0.00	11.39	−0.06	14.56	−0.16	17.94	+0.01	21.86	+0.13	.....	.....
300	11.25	+0.01	12.82	+0.07	16.21	−0.15	19.88	−0.01	24.19	+0.05	.....	.....
420	13.06	+0.04	15.46	+0.30	19.00	+0.15	23.06	+0.15	27.94	−0.14	.....	.....
540	14.60	−0.05	17.85	−0.02	21.29	+0.38	.....	.....	.....	.....	.....	.....
660	16.04	−0.01	20.05	−0.30	.....	.....	.....	.....	.....	.....	.....	.....
780	17.31	+0.04	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....

In order to measure the absorption rates under equal conditions within the seeds, it is essential to compare velocities of absorption at a time when the seeds have absorbed equal quantities of water above the air dry condition. By reference to fig. 1, it will be seen that six levels of intake have been chosen for tangent measurements. These are indicated by the horizontal lines, where the intake, y, is 7.5, 10, 12.5, 15, 17.5, and 20 per cent above the air dry condition of the seed. In table IV is shown the length of time in minutes required to reach each level of intake at which the tangents were measured, together with the rate of intake at the moment when

the curves pass the tangent points. The rates of absorption per minute are expressed in percentages of the original dry weight of the seed. Table IV shows how the time required to reach a given stage of absorption is decreased by rising temperature, and the intake rates show how the rate falls off with increasing absorption at any given temperature.

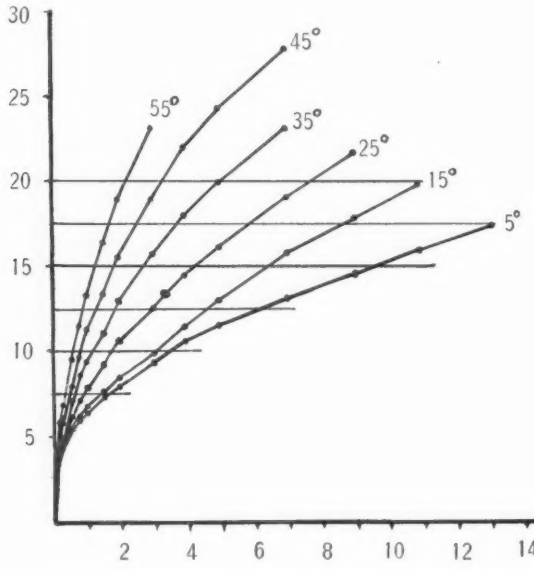

FIG. 1.—Absorption curves for corn at various temperatures: abscissae, time in hours; ordinates, percentage of water intake.

From the intake velocities of table IV, the ratios of the velocities at equal intake levels for 10° differences have been computed. These ratios are the temperature coefficients of absorption, Q_{10}, and are presented in detail in table V.

The average value of Q_{10} (the average of the averages for each series at the bottom of the table) is 1.537, which is very slightly less than the 1.55 obtained in the case of *Xanthium* seeds several years ago. The rapidly increasing ratios in the column 15°/5°,

and the correspondingly falling series of ratios 25°/15°, are caused by the peculiarities of the 15° curve, referred to earlier. The intake was relatively too slow during the earlier phases of intake, and too rapid later on to fit properly between the 5° and 25° curves. Inspection of the two series shows that the 15° curve passed through its

TABLE IV

RATE OF ABSORPTION IN CORN; TIME EXPRESSED IN MINUTES; RATE IN PERCENTAGE OF INTAKE PER MINUTE

PERCENTAGE INTAKE	TEMPERATURE											
	5°		15°		25°		35°		45°		55°	
	Time	Rate	Time	Rate	Time	Rate	Time	Rate	Time	Rate	Time	Rate
7.5..	98.06	0.02157	92.11	0.02835	55.82	0.05103	35.22	0.07866	26.55	0.11676	18.43	0.16674
10.0..	225.08	0.01777	184.65	0.02577	109.90	0.01201	70.30	0.06176	49.07	0.00781	34.75	0.14111
12.5..	381.60	0.01464	286.42	0.02343	175.59	0.04459	112.91	0.05332	77.75	0.08202	54.03	0.11943
15.0..	569.78	0.01266	398.41	0.02130	255.35	0.02848	164.68	0.04389	111.32	0.06863	76.81	0.10108
17.5..	798.52	0.00993	521.57	0.01936	352.22	0.02345	227.55	0.03614	151.18	0.05749	103.73	0.08554
20.0..	1076.25	0.00818	657.06	0.01766	470.02	0.01930	303.92	0.02975	198.75	0.04816	135.54	0.07239

TABLE V

TEMPERATURE COEFFICIENTS OF WATER ABSORPTION IN CORN

PERCENTAGE INTAKE	VELOCITY RATIOS AT GIVEN PERCENTAGE OF INTAKE				
	Velocity 15° / Velocity 5°	Velocity 25° / Velocity 15°	Velocity 35° / Velocity 25°	Velocity 45° / Velocity 35°	Velocity 55° / Velocity 45°
7.5	1.314	1.800	1.541	1.484	1.428
10.0	1.450	1.630	1.541	1.510	1.443
12.5	1.602	1.476	1.541	1.538	1.450
15.0	1.766	1.337	1.541	1.564	1.473
17.5	1.950	1.211	1.541	1.591	1.488
20.0	2.152	1.097	1.541	1.619	1.503
Average	1.706	1.425	1.541	1.551	1.465

normal position at an intake of about 11 per cent. On several other occasions irregular absorption behavior has been observed at 15° C. This is probably mere coincidence, however. The data are too meager to justify the suggestion that the irregularities may be due to a critical temperature relation. Individual peculiarities, including differences in absorptive capacity, will no doubt account for all the irregularities observed.

Discussion

The quantitative study of absorption is beset with numerous difficulties, not the least of which is the variability of the absorbing material. The early intake data of table I show that corn grains are somewhat irregular in moisture intake during the first fifteen to thirty minutes, regardless of strict control of the conditions. After that time the intake is fairly uniform, barring internal physical changes. The behavior suggests that there is a certain amount of heterogeneity in the substance of the grains, which may bring about irregular absorption through variations in the quantity of the components present in individual seeds, the components themselves possibly having different absorption rates at the same temperature. After a time the intake becomes regular, and the temperature influence becomes visible. Our quantitative studies in this case deal only with the main curve, after the initial irregularities have disappeared.

So many cases of irregular absorption have been observed during the last ten years that one might be inclined to think that the cases which can be analyzed mathematically with any degree of exactness are the exception, not the rule. Sometimes the changes in the rate of absorption are so great that analysis becomes impossible, or meaningless, and would require tangent sectors of different types of curves to follow the data. Moreover, after such sectors had been worked out, it is possible that they could not be interpreted. The irregularities of intake result from a number of causes which may be briefly touched upon.

Heterogeneity is a rather common cause of irregular behavior, especially in seeds, where coats, embryos, and endosperm of different kinds may possess widely different physical and chemical constitution. If the seed coat is very porous, embryo moderately absorptive, and endosperm very hard and resistant, the absorption rate will be changed as each part absorbs its quota of water. In some cases impermeability of the coat may cause abnormal results. The hard seeds of legumes may be cited in this connection. In one experiment with beans, an individual seed lay for three days immersed in water before significant intake began. One such seed in an experimental group would cause the mathematician much trouble.

Another potent cause of irregularity was pointed out in the work on pea cotyledons. Internal breaks are of frequent occurrence. After running along uniformly for an hour or two, intake shows a sudden increase, the absorption for a given period being perhaps twice what one would expect from the preceding portion of the curve. In such cases, on careful inspection of corn grains one can often find cracks in the endosperm which are visible through the unbroken coat. The formation of the internal cavity sets up a partial vacuum, into which unabsorbed water is drawn. A number of carefully run series had to be discarded on this account. Accurate analysis would have been impossible.

Internal structure may modify absorption rates to such an extent that the data are not a measure of absorption as such. This is the case in dealing with absorption by small blocks of wood. Cubes of cherry wood not more than a few millimeters in diameter were kept immersed in water at 25° C., and, small as they were, it required from fifteen days to a month or more for them to reach their maximum weight. It is evident here that it is not simple absorption of water by wood that is being measured. The tracheae are full of air, and on immersion the water cannot enter and displace the air, but merely enters the open ends of the tracheae, and penetrates through the walls where there is no air to displace. The long, slow absorption period is probably dominated by the solution of the gas, as in waterlogging, and the data do not reveal the absorption rate of the wood substance. If the blocks are first strongly evacuated, and water introduced over them while in this condition, considerable water enters at once, and the whole curve of increasing weight is changed.

One of the most interesting cases of irregular absorption behavior was found in the tissue of *Auricularia*. Square pieces of the fungus were allowed to dry, giving pieces about 8 mm. square and 0.5 mm. thick. One of these pieces weighed 0.0242 gm. Immersed in water at 25° C., it required twelve days to reach its maximum weight, at which time the increase in weight was 2310 per cent. The rate was not uniform during the period, nor did the rate decrease in orderly fashion with time. In the first two minutes the intake was more than 100 per cent, mainly from the porosity of the outer layers of the tissue. During the first twenty-four hours the total

absorption was 455 per cent, and in the second day it was 78 per cent. The rate of intake remained at about that level for a day or two, and then began increasing again. On the fifth day it was 129 per cent, the sixth day 160, and the seventh day 279 per cent. During this second rapid period of weight increase, the middle layer of the fungus tissue became clear, gelatinous, and highly swollen. Finally the piece split apart through the middle layer. In this case it seems highly probable that the rate of absorption is partially determined by chemical changes, perhaps in the nature of transformation and hydration of polysaccharide carbohydrates. After the tissue had passed the maximum point of increased weight at the end of twelve days, it was allowed to become air dry again. On reweighing, it was found to have lost 31 per cent of its weight during absorption. This behavior reminds one of the results obtained by MACDOUGAL, RICHARDS, and SPOEHR (10, 11), with other biocolloids, discs of cacti, etc.

These irregularities of behavior often make the problem of interpretation difficult, and one must expect specific behavior in all kinds of objects, depending upon structure, composition, physical and chemical behavior of the materials used. It follows, also, that there is probably no rate law for absorption. The fact that a single type of curve has been successfully fitted to the absorption data of several types of seeds is not sufficient evidence for a rate law, but merely shows that when conditions are uniform inside and outside the absorbing body, the processes of water absorption proceed regularly, in accordance with the physical and chemical forces operating.

One of the problems connected with the investigation of absorption rates, particularly in the seeds of the Gramineae, is the localization of water intake by the investing membranes of the caryopsis. COLLINS (7) studied absorption by barley grains, and came to the conclusion that there are localized areas at the germ end of the grain through which most of the water passes. Using iodine solutions to render the progress of intake visible, he drew the general conclusion that "the entry of iodine solutions into the barley grain is not general and uniform over the whole surface of the grain, but its uptake is localized at the germinal end, and it is distributed periph-

erally in the endosperm along the subaleuronic layer of starch cells of the curved surface." Tests with acids and stains seemed to confirm the idea that both water and solutes gain entry in the micropylar region through a selectively active tract of cells which constitute a specialized local path of entry.

The same general conclusion was reached by HARRINGTON and CROCKER (9), who studied the entry of iodine solutions into the caryopses of Johnson grass and Sudan grass. The solution seemed to enter through the hilar orifice, or micropyle, or both, and to spread in a distal direction along the inner surfaces of the aleurone layer and scutellum.

Preliminary studies made on corn at the University of Kansas indicated general permeability of corn seed coats to water. LOVEJOY'S osmosis tests were made with coats taken from the main lateral areas of the grain; and these were not only permeable to water, but also allowed salts used as solutes to pass out slowly during the exhibition of osmotic action. These facts point to coat permeability to both water and salts. Some iodine tests made at the University of Kentucky indicated that the coats of corn allow iodine also to penetrate the surface of the grain generally, a fact observed by HARRINGTON and CROCKER. The entry in the case of Hickory King corn, however, appears to be more rapid over the flank surfaces than over the distal areas of the coats. Water also enters with considerably greater rapidity through the proximal portions of the integuments, even when the micropylar and hilar areas are sealed over. These iodine studies (1) indicate that COLLINS, and HARRINGTON and CROCKER have possibly misinterpreted the progressive distalward staining of subaleuronic tissues with iodine. The evidence is clear in the case of corn that there is very little transfer of iodine through the tissues in any direction, but that the iodine is adsorbed or chemically combined as it enters, and is not very free to travel through the tissues. The appearance of distalward movement in barley is undoubtedly due to differential permeability of the caryopsis integuments, the iodine penetrating more rapidly over the proximal regions, and progressively less rapidly toward the distal end of the grain. This gives, with time, the appearance of a distalward movement of iodine in the subaleurone region,

which in reality does not take place. This situation has been demonstrated for wheat by BRAUN (**2**) at the Cincinnati meeting of the Botanical Society of America. His work and the work done in the Hull Botanical Laboratories on this point are in general agreement.

Since REICHARD (**13**) had associated the semipermeability of barley seeds with a tannin layer, some microchemical tests of corn were made, on both yellow and white corn seed coats. The tests showed only minute amounts of tannin present in isolated cells or groups of cells. No evidence of a tannin layer was found, so that any semipermeable properties present do not depend upon tannins. In this connection it should be noted that COLLINS was not able to confirm REICHARD'S claim of a definite tannin layer in the barley grain.

The main purpose of this work was to put the chemical theory of water absorption proposed by BROWN and WORLEY (**6**) to a crucial test. If absorption is determined as to rate by chemical simplification changes in water, the polyhydrones dissociating as the temperature rises and providing larger quantities of simple hydrone which alone can pass the membranes, and if it has a temperature coefficient of two or above, then a rise of 50° C. should result in a rate of intake about thirty-two times as great at the highest temperature as at the lowest of the range used. If the increase were not so large, the amount by which it fell short would be a general measure of the failure of the theory.

The total increase in absorption rate for the 50° rise can be obtained from the ratio $50°/5°$, or the five average ratios of table V may be multiplied into one another successively. By either method it is found that the rate of water intake at 50° C. is somewhat more than eight times as rapid as at 5° C., instead of thirty-two times as great. In other words, the increase in absorption brought by a 50° rise in temperature is only about one-fourth as much as would be expected if the process were determined by some chemical change, as has been proposed. The results are strongly against the chemical hypothesis.

Attention is also called to the fact that the values of Q_{10} in table V show little if any tendency to decrease at high temperatures,

as one might expect from the Arrhenius temperature law, if we are dealing with a chemical process. While the formula upon which the Van't Hoff rule is based does not provide for a smaller temperature coefficient as the temperature rises, the more correct formula of the Arrhenius law shows from its plotted curve (**12**) that the value of Q_{10} tends to decrease at high temperatures. Biological processes involving chemical changes frequently show reduction of the temperature coefficient as the temperature becomes extreme. In some cases these results are caused by the harmful action of heat upon the protoplasm; but such reductions at high temperatures are in agreement with the Arrhenius law, and would be expected even if the protoplasm were to remain unharmed by the heating. While our results are made irregular by a poor 15° curve, the average value of Q_{10} at the highest temperature used is still higher than the values at 25° and 35°, and only slightly below that at 45°. There is no striking tendency to decrease as shown in these figures, and very little should be expected if we are dealing with a process largely non-chemical in nature.

The data as a whole constitute additional evidence in favor of the point of view developed in previous work, that absorption is as complex as many other life processes, and involves both physical and chemical factors. The fact that the value of Q_{10} is not so very much above the coefficient for physical processes should indicate that it is mainly a physical process, as has always been assumed. Furthermore, it seems very probable that temperature effects upon the seed colloids account satisfactorily for the slightly higher value of the temperature coefficient for absorption in corn.

Since it has been possible to run these curves very close to the experimental data with the same logarithmic formula as was used with *Xanthium* seeds and split peas, it is clear that the data are adverse to the idea that the velocity of absorption is an exponential function of the temperature. Whenever it is possible to apply the equation used in this paper to the curve of absorption, the velocity is determined by the previous absorption, rather than by temperature. The formula which expresses this relation has been given in the introductory paragraph. The corn absorption is then another case in which the velocity of intake at any moment is an

inverse exponential function of the total previous intake. In discussing the problems of permeability, STILES (**18**) remarks that, aside from the precision in measuring tangents, and from them the velocity of absorption, such formulas as the equations used to represent the curves of water intake in this work do not tell us much about the nature of absorption and permeability. This critical judgment of the method is well taken; and the only use we originally had for the formulas was to substitute precise methods for rough methods of measuring tangents. For that purpose any regular mathematical expression that followed the data faithfully could have been used with equally precise results. It would be hard to find a mathematical formula that serves this purpose any better than the one here used. The only other conclusion that we reach from the mathematical expression used is the conclusion as to the velocity being an inverse exponential function of the previous absorption; and that conclusion is implicit in the formula used, a conclusion made necessary by the nature of the equation. The conclusion that the process of absorption is physical mainly rests on the Q_{10} values, which would have been the same if calculated from any other curve following the same data.

In BROWN and WORLEY'S theory of water intake, the semipermeable membrane had an important rôle in determining the rate of water penetration. It was held that only simple hydrones could pass through such a membrane, while the complex polyhydrones or associated H_2O groups would be held back. Water absorption through semipermeable seed coats, however, has about the same temperature coefficient as absorption in the absence of a membrane. This makes it improbable, as was previously stated, that semipermeability is important in determining the rate of absorption of water, *when supplied as distilled water.*

During the last twenty years the fact that many seeds are provided with selectively permeable coats has become well established in the literature (**3, 4, 8, 15, 16**). An occasional paper appears, however, in which the significance of this fact seems to be overlooked, and it is advisable to lay emphasis upon the presence in seeds of osmotic membranes, capable of showing the same behavior toward solutions as do membranes of living protoplasm.

In all cases where such membranes are present, they will affect the rate of water intake if water is supplied in the form of a *solution*, whether of nutrient or non-nutrient salts.

This seed coat condition, for instance, accounts for a large part of RUDOLFS' (**14**) results, although he mentions none of the pertinent literature. The behavior which he describes is exactly what would be expected of seeds possessing semipermeable coats, and has exactly the same significance as the fact that a saturation deficit can be produced in a living cell possessing a semipermeable protoplasmic membrane, by means of KNO_3 solutions. Of nine kinds of seeds used by RUDOLFS, six are from families in which semipermeable coats have been described. The mere fact that nutrient salts were used does not change the nature of the phenomenon. In the cases where absorption seems to be increased above normal by salt action, the formation of soluble organic materials within the semipermeable seed coat may account for the results, or we may be dealing with membrane equilibria. In *Xanthium* seeds the formation of osmotically active solutes inside the seed leads to excessive water intake. This is particularly true with KOH and acetic acid. Possibly the behavior of K_2CO_3 in RUDOLFS' work is to be explained mainly on the basis of the hydrolysis of the salt, the production of KOH, and the internal effects of KOH on the seed substance, coupled with semipermeable coat effects. This problem has received critical consideration by BROWN and TINKER (**5**) with reference to phenols and acetic acid.

The work presented here confirms in detail the results obtained several years ago with seeds belonging to families far removed from the Gramineae. The mere fact that seeds of *Xanthium* are fatty, peas rather high in protein, and corn rich in carbohydrates, has little to do with the physics of absorption. It may have something to do with the total amount taken in at saturation, for corn saturates at more than 60 per cent, *Xanthium* at a little over 50 per cent, peas at 75–90 per cent (according to the variety), and some other legumes at still larger amounts; but the velocity apparently is determined by physical factors largely, with the state of the colloids modifying to a certain extent the rate of water entry.

Summary

1. A study of the influence of wide temperature differences on the rate of water absorption by seeds of corn has been made, with results in complete agreement with a similar study of *Xanthium* seeds and pea cotyledons made previously.

2. The same type of formula, and the methods of mathematical analysis used with other seeds, were found to apply with great exactness to the data obtained with corn.

3. The temperature coefficient over the range from 5°–50° C. averages 1.537, somewhat above the coefficient for purely physical processes. This coefficient is to be compared with that of 1.55 for *Xanthium* seeds, and 1.6 for pea cotyledons.

4. The rate of absorption at 50° C. is somewhat more than eight times as fast as at 5° C., whereas the chemical theory of absorption would call for a rate thirty-two times as great.

5. The increase is therefore only one-fourth of what one would expect if absorption rates were determined by hydrone simplification of water as the temperature rises.

6. From mathematical considerations, the velocity of intake at any given moment must be considered as approximately an inverse exponential function of the amount of water previously absorbed.

7. Attention is called to a number of cases of irregular absorption rates, which indicate that many substances have specific absorption behavior. A rate law with wide applicability is not to be expected.

8. The importance of semipermeability with reference to the intake of water from solutions of various kinds is pointed out.

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EMBRYOGENY OF ABIES

A. H. Hutchinson

(WITH PLATES XVII–XX AND THREE FIGURES)

This investigation of the embryo development in *Abies* was begun during the summer of 1914. Since that time much additional material has been collected, in order that gaps might be filled in the series and that no stages might be omitted. The most complete series is that of *Abies balsamea* collected in Algonquin Park, Ontario, but sufficient sections of *A. grandis* and *A. amabalis* have been made to establish the similarity of these species with respect to the development of their embryos. Miyake (**8**) studied the early stages of the proembryo of *A. balsamea*, and his figs. 35–40 show that the development up to the eight-celled stage is similar to that of *Pinus*. Buchholz (**1, 2**) states that *Abies* "probably has proembryos identical with *Pinus*," and that "in a few rare instances a divided rosette cell and a more advanced rosette embryo were found; cleavage polyembryony was found in a few cases." Beyond this stage no records are available.

Proembryo

In an earlier paper (**6**) the first division of the zygote nucleus has been described. The first and second free nuclear divisions occur during the time the proembryo is moving from the central area of the egg cytoplasm to the pole remote from the micropyle. During the late telophases and until the early prophases the nuclei are quite large, 40–50 μ in diameter, and show vacuolated chromatic strands (text figs. 1–3). At the time of fertilization the egg cytoplasm is filled with large and abundant food bodies, chiefly starch grains. This food is rapidly digested and utilized to such an extent that when the four nuclei have reached the abmicropylar pole, the cytoplasm, which has accumulated in the same region, contains only a small residuum of finely granular food material surrounding the nuclei. The next divisions result in two tiers of

four cells each, the abmicropylar cells containing the greater portion of the remaining food store, while the nuclei of the open cells have a very limited supply (figs. 3–6). It seems probable that this condition may be a determining factor in the modification of succeeding stages of development.

FIG. 1.—Embryo of *Abies* surrounded by gametophyte

Ordinarily the proembryo development ends at the eight-celled stage, the four abmicropylar cells being primary embryo cells and the admicropylar four resembling the open tier of *Pinus* (figs. 3, 5, 6, 7). Out of many, only three cases were found where a third tier was interposed, and in these instances the cells were scantily supplied with cytoplasm, platelike in form, and suspended in the open region resulting from the rapid movement of the primary

embryo cells toward the abmicropylar gametophyte tissue. Whether this interposed tier is homologous to the suspensor cells or to the rosette cells can only be conjectured, largely because of their infrequent occurrence and their temporary nature. Moreover, no divisions have been found in the open tier of cells, and since the movement of the abmicropylar cells begins very soon after their formation, it is difficult to determine whether the division of the tier in any given case is about to result in the production of primary embryo cells and suspensor cells, or of the cells of the embryo and embryonal tubes. It is remarkable that, with few exceptions, neither rosette nor suspensor cells are formed. The nuclei of the open tier rapidly disintegrate, while the primary embryo cells move into the gametophyte tissue and continue digestive and mitotic activity.

FIG. 2.—Embryo of *Abies*, showing early stage in development of cotyledons.

Cleavage polyembryony

Cleavage polyembryony occurs in approximately 10 per cent of the cases studied (figs. 8, 9, 11). Not infrequently as many as four embryos reach the eight to sixteen-celled stage before elimination through competition begins (fig. 8). Cleavage of the primary embryo cells depends directly upon the completeness of the fiber system formed during the eight-celled stage. In some instances the fiber area reaches to the tip of the proembryo (fig. 5), but more frequently it forms an incomplete plate between the primary embryo cells (fig. 3), and in some cases this plate seems to be absent. Where complete cleavage does not take place there may be a variable degree of separation at the admicropylar end of these

cells (figs. 6, 7). The wall does not form in the ordinary way along the central axis of the fiber mass, but instead a membrane is laid down at the margins of the fiber area, and as the fibers disintegrate the delimited area remains as an open intercellular space. In the reduced proembryo of eight cells the fibers between the two tiers of cells have a similar history. In this manner the primary embryo

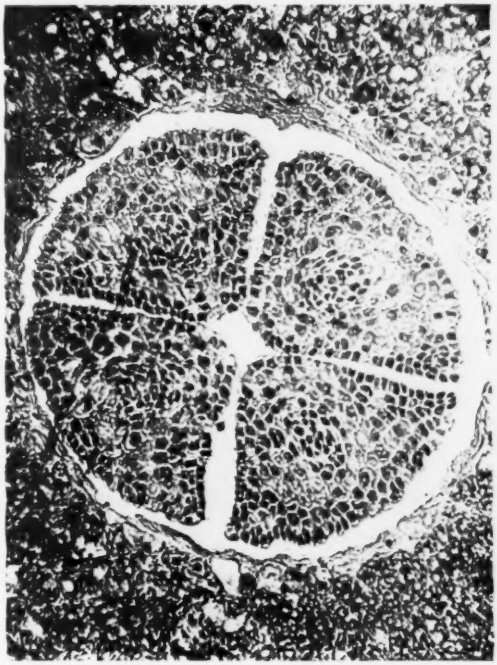

FIG. 3.—Transverse section of cotyledons of *Abies*

cells become free to move into the gametophyte tissue (figs. 3, 5, 6, 7). There is evidence that cleavage polyembryony in *Abies* is the result of this peculiar development of detached pairs of adjacent cell walls during the mitoses of the proembryo.

Intercalary growth of embryo

The early growth of the embryo is linear. The division of each primary embryo cell is followed by a number of intercalary divisions

in the same direction. In embryos where cleavage has been initiated in the proembryo the result is a filament of six or eight cells (fig. 9), several of which have elongated to form embryonal tubes, otherwise there are four (or sometimes two) chains of cells joined to form a single embryo, each chain elongating by intercalary divisions (figs. 8–14). Fig. 13 shows a case where an admicropylar cell of one series has divided first, while the abmicropylar cell of the other series has been first to divide. The only cells which do not divide are some of the admicropylar which develop into embryonal tubes. It is during this period of intercalary growth that the embryo moves most rapidly in the abmicropylar direction.

Formation of massive embryo

Linear, intercalary growth with the formation of transverse walls is followed by divisions, the walls of which are in the direction of the main axis (figs. 9, 11, 14, 16). The filamentous embryo, resulting from cleavage of the proembryo, is thereby converted into an embryo of four series of cells, which resembles the preceding stage of an embryo where no cleavage has taken place (fig. 11). Periclinal walls are formed next, producing central and peripheral areas (figs. 15, 17). These regions are the primary structural units, and their identity is maintained throughout the development of the embryo. The peripheral layer, or protoderm of HABERLANDT (5), is the first region to become differentiated. The cells of this layer covering the abmicropylar end of the embryo divide only by anticlinal walls, giving origin to the epidermis; whereas the cells at the admicropylar end divide in all planes but most rapidly in the plane of the longitudinal axis, thereby giving origin to the massive structure which at first is suspensor-like in function, and which later becomes the coleorhiza and root cap, successively (fig. 18). The cells of the central area divide at a fairly uniform rate in all planes, thereby producing a globular mass of undifferentiated cells (fig. 18). The admicropylar elongation at this stage is accompanied by an abmicropylar movement of the embryo and by a rapid disintegration of the terminal cells. The embryo at this time is decidedly club-shaped.

Mitotic activity

The primary differentiation of the embryo may be expressed almost entirely in terms of mitotic activity. As already noted, the protoderm is the first region where the planes of division are limited in number, and the regularity of these divisions gives rise to the epidermis and coleorhiza. The cotyledons are the result of decreased or suppressed mitotic activity at the abmicropylar end of the longitudinal axis, accompanied by constant or increased activity at the marginal region surrounding this area. The nuclei of the former region are in the resting condition, as shown by their many nucleoli, whereas the commonly occurring mitotic figures in the latter region give evidence of both dermal and subdermal activity. Inequalities in this activity produce lobes or the primordia of cotyledons (figs. 19, 20). The number of these areas of increased mitotic activity and hence the number of cotyledons varies about the mean of four or five. At this time the cells of the embryo are all nearly isometric, and there is no apparent differentiation of the cytoplasm. Another area of suppressed mitotic activity is found at the admicropylar end of the central area in contact with the developing root cap (fig. 21). This group of cells is similar in position and general conformation to those cells which many have called the "initials." These have shown repeatedly, however, the same resting characteristics as the dormant stem tip cells, whereas the cells surrounding them are mitotically active. When the cotyledons have attained approximately one-half their mature length the procambial strands begin to appear. In some instances they may be detected in the admicropylar or radicle region first, but ordinarily their appearances are simultaneous from the margin of the region of suppressed activity at the tip of the radicle to the terminal region of the cotyledons. The procambial strands are composed of cells which resemble the cambium in mode of division, that is, their walls are in the direction of the longitudinal axis only. The tension resulting from transverse divisions in the adjacent cells causes the elongation of the procambial cells.

In following the development of primary morphological units in the embryo of *Abies*, one is forced to the conclusion that these

units are not functional primarily, but are the result of the nature and degree of mitotic activity, and later they perform some function or other. The epidermis arises as a peripheral region of anticlinal walls and becomes a single-layered, absorptive and later a protective region. The root cap arises as a peripheral region of periclinal divisions chiefly, and becomes a suspensor and later a protective region. The cotyledons arise as regions of augmented mitoses and become food storage organs and later a source of food. The stem tip arises as a region of suppressed mitotic activity and later becomes the most marked of growing regions. The procambial strands originate as regions of axial divisions, and by similar divisions continue to give rise to conductive cells. The little explored field of investigation which deals with the factors determining the nature and rate of mitosis is basic to any explanation of embryo development.

Discussion

The events of the very early proembryo as described in this paper confirm the account of MIYAKE (**8**). There is, however, a very marked difference between the later embryos found in my specimens of *Abies* and those described by BUCHHOLZ (**2, 4**). The latter states that "in *Abies* the normal product of a fertilized egg is a single embryo. The group of rosette cells is present, and in a few rare instances a divided rosette cell and a more advanced rosette embryo were found." On the contrary, cleavage polyembryony frequently occurs in *Abies*, a distinct separation being evident in 10 per cent of the instances and an incomplete cleavage in a large proportion of those remaining. No rosette has been found, but vestiges of what may be regarded as rosette cells were seen (fig. 4), and it is not probable that these would have been seen in the dissected embryos studied by BUCHHOLZ. The fact that an embryo sometimes begins to develop from the fertilized ventral canal cell (**6**), together with the difficulty which BUCHHOLZ found in clearly distinguishing the cells which he describes as rosettes, may explain the apparent contradictions. To quote: "The basal plate, a deposit formed within the egg over the rosette cells, is very thick and frequently obstructs a clear view of the rosette cells, which also collapse early unless a rosette embryo

happens to develop." The embryos of *Abies* which I have examined resemble those described for *Pseudotsuga* (**4**) more nearly than those of any other conifer.

The peculiar mitotic figure described by Miss KILDAHL (**7**) for *Pinus* in the proembryo is similar to those occurring in *Abies*. In *Pinus* the plate of the unusual fibers is axial in direction, and may be regarded as accounting for the cleavage polyembryony, as in *Abies*. In *Abies* similar structures with resulting walls are formed transversely, thereby making possible the movement of the primary embryo cells away from the open tier.

The embryo of *Abies* shows many advanced characters, chiefly in the form of reduction and the elimination of ancestral or primitive features, notably the rosette cells, suspensor cells, and the apical cell. Another feature which may or may not be advanced is the occurrence of cleavage polyembryony. BUCHHOLZ regards this as a primitive character. Primitive characters are usually constant features of lower orders or even of divisions, such as is the case with suspensors and apical cells, or are present in geologically more ancient forms, but on a basis of such evidence there is no reason to suppose that cleavage polyembryony is primitive. Moreover, *Abies* furnishes rather satisfactory evidence that cleavage polyembryony is a derived condition. Ordinary cell divisions in the proembryo result in single embryos, while modified divisions (figs. 5–7) result in cleavage of the proembryo. It may be noted also that the proembryos which are most reduced in the number of cells show cleavage, while those which are less reduced (fig. 4) do not show cleavage. To concede that cleavage polyembryony is a derived character does not affect the position of *Pinus* necessarily, since it has very frequently been demonstrated that living forms of remote lineage exhibit a complex of derived and of primitive characters. In any event, it may be conceded that the proembryo and early embryo of *Abies* are advanced or derived in many respects.

Summary

1. The proembryo of *Abies* ordinarily consists of eight cells only, in two tiers, the admicropylar open tier and the abmicropylar primary embryo tier of cells.

2. Very infrequently a third tier is interposed, which may represent the rosette or the suspensor.

3. Cleavage polyembryony frequently occurs, and is the result of modified spindle structures.

4. The early embryo grows by intercalary divisions; an apical cell is not formed.

5. Primary periclinal divisions delimit the central region from the protoderm; these regions persist as primary structural units.

6. Regions which become tissues are differentiated primarily because of specific mitotic characters and later assume functional characters.

7. The stem tip and the "initials" are regions composed of resting cells in the early embryo.

8. The embryo of *Abies* shows many advanced or derived characters.

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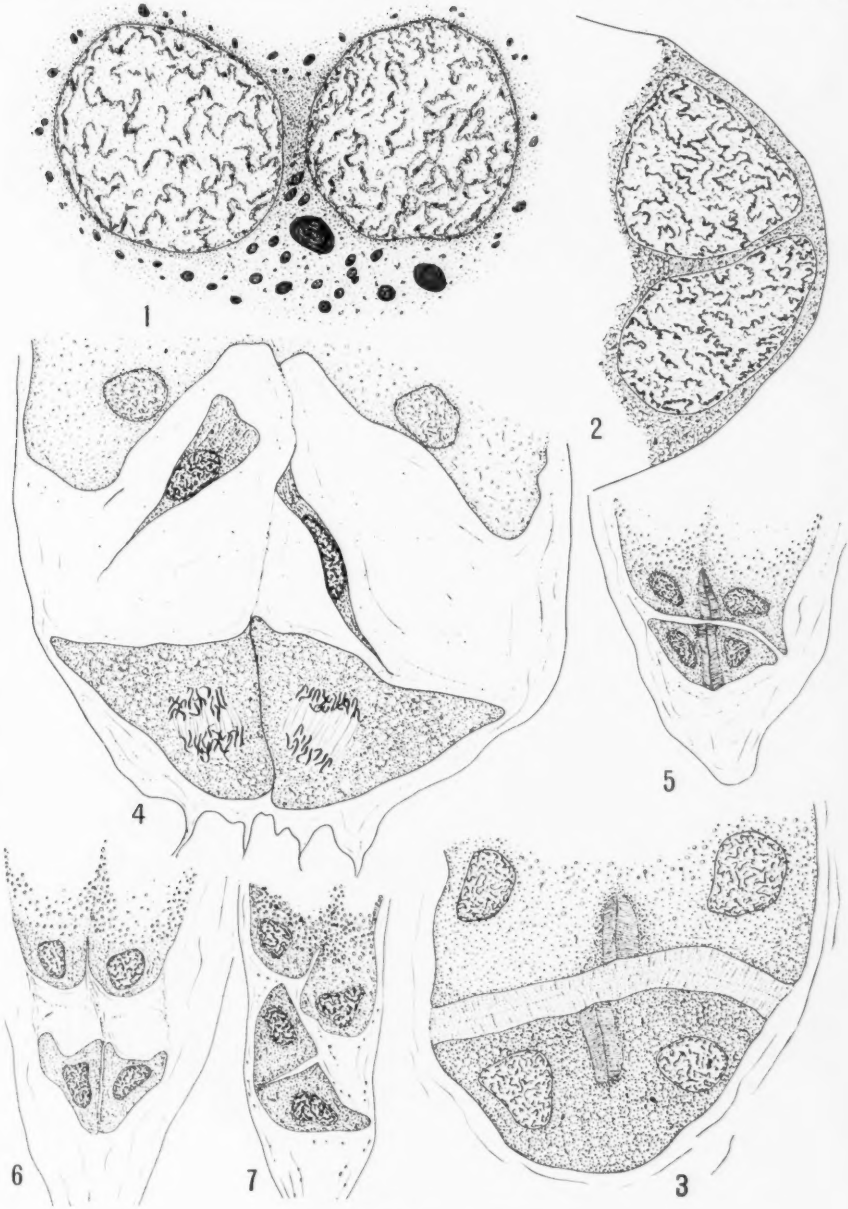
DESCRIPTION OF PLATES XVII–XX

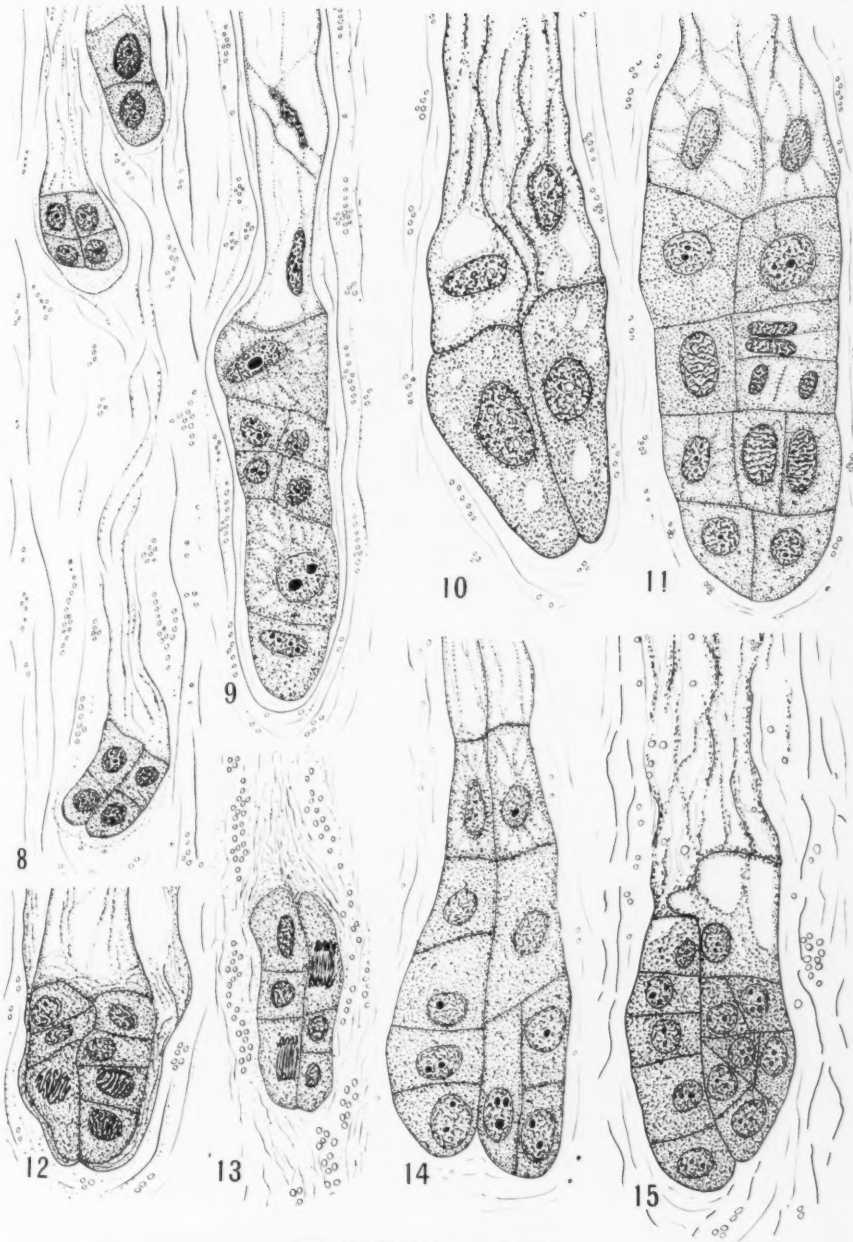
All figures are drawn with the aid of a camera lucida.

FIG. 1.—Nuclei resulting from first division of zygote, imbedded in egg cytoplasm.

FIG. 2.—Two of the four nuclei which have migrated to abmicropylar end of egg cytoplasm.

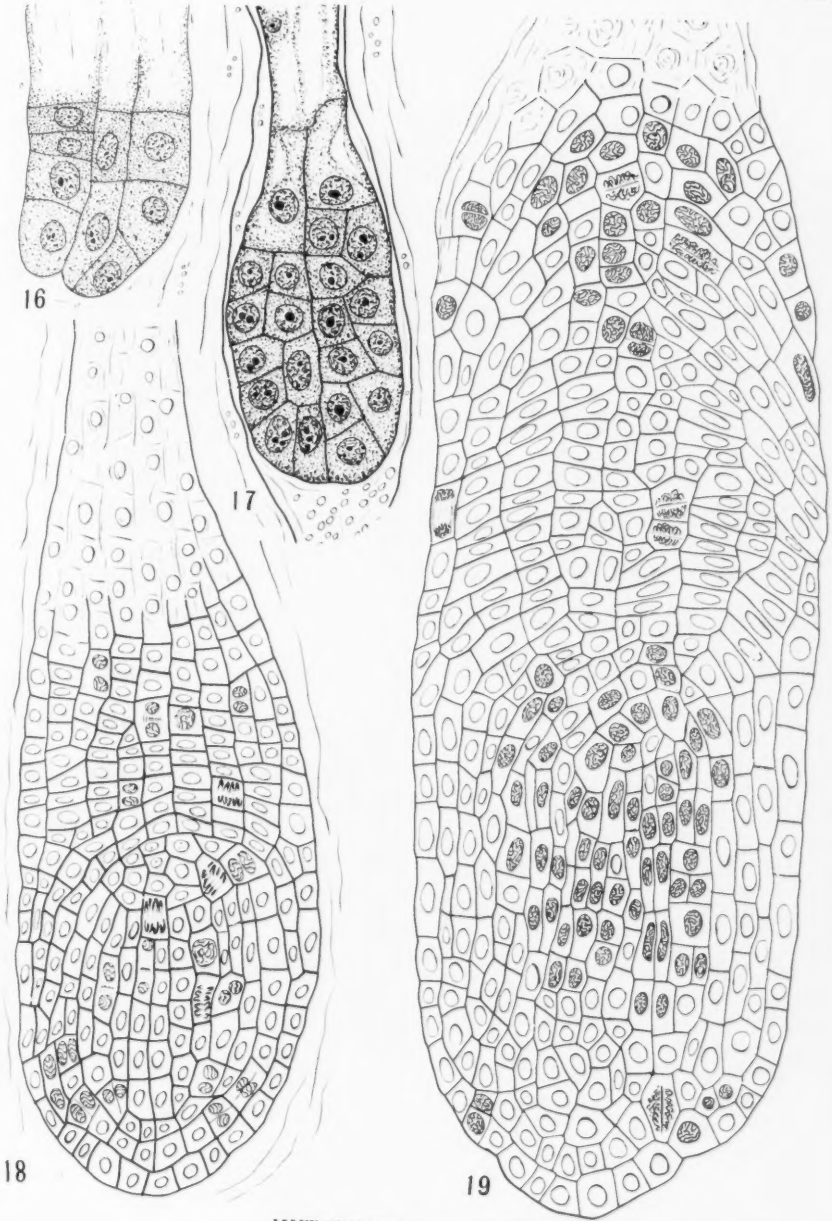


HUTCHINSON on ABIES

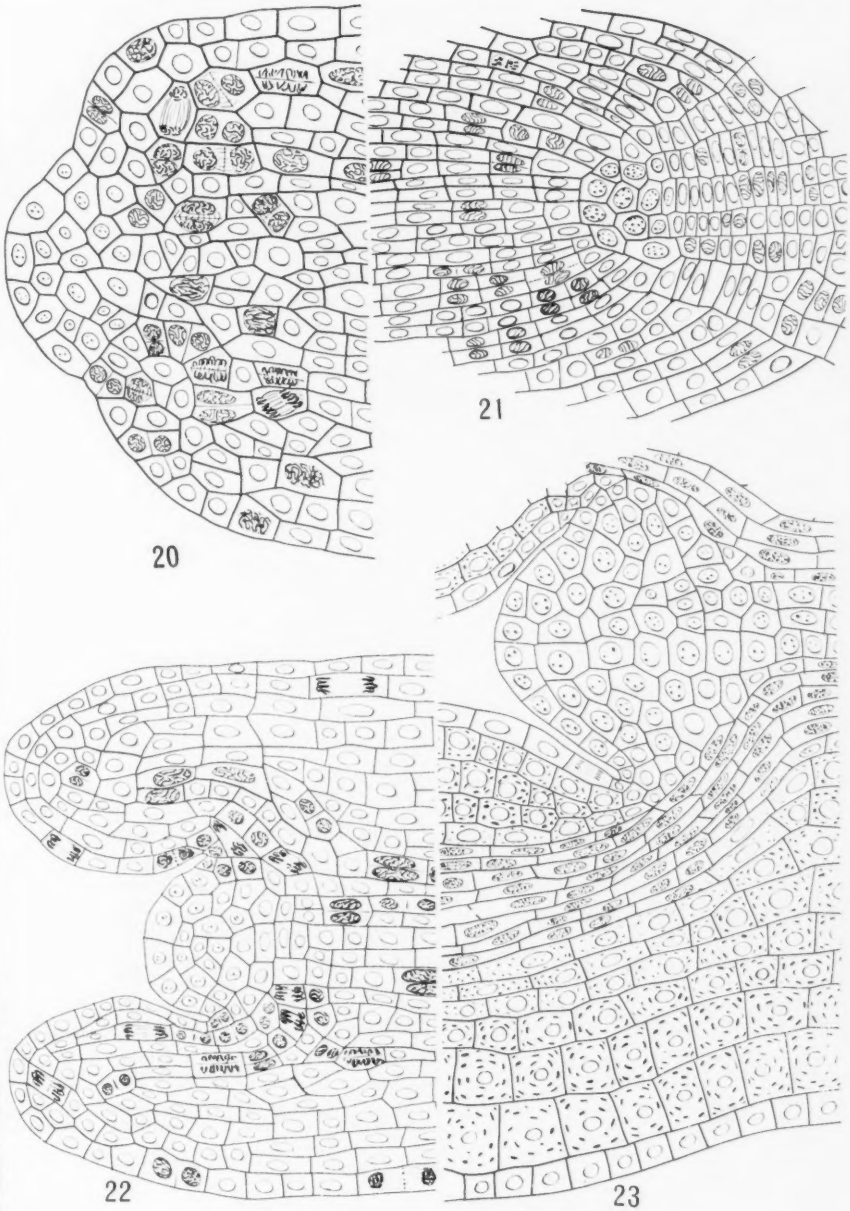


HUTCHINSON on ABIES

PLATE XIX



HUTCHINSON on ABIES



HUTCHINSON on ABIES

FIG. 3.—Eight-celled stage which proves to be complete proembryo in most instances, showing primary embryo cells and open tier; note transverse plate of disintegrating fibers and two parallel walls separated by fiber area, also axial fiber plates, incomplete.

FIG. 4.—Unusual embryo, showing vestigial cells interposed between open tier and primary embryo cells; latter have moved some distance in abmicropylar direction and are dividing to form terminal embryo cells and embryonal tubes.

FIG. 5.—Proembryo in which transverse plate of fibers has disintegrated, releasing primary embryonal cells; axial plate is complete as in cases of cleavage polyembryony.

FIGS. 6, 7.—Primary embryo cells moving away from open tiers.

FIG. 8.—Three of four embryos which have resulted from cleavage of proembryo, surrounded by food material derived from gametophyte; embryonal tube cells rapidly disintegrating; axial divisions already taken place in two embryos.

FIG. 9.—Embryo which has resulted from cleavage of proembryo and which formed filament of eight or more cells before axial walls were formed.

FIGS. 10, 12, 13.—Embryos composed of four series of cells.

FIGS. 11, 14, 15, 16.—Appearance of periclinal walls.

FIG. 17.—Primary periclinal walls complete, thereby delimiting primary central and peripheral regions.

FIG. 18.—Massive embryo; peripheral region (protoderm) showing two areas, abmicropylar with anticlinal divisions only, admicropylar with periclinal divisions chiefly; central region undifferentiated.

FIG. 19.—Massive embryo, similar to fig. 18, except that increased mitotic activity is giving rise to cotyledonary protuberances.

FIG. 20.—Increased mitotic activity in region of cotyledonary outgrowths associated with resting condition of cells at abmicropylar tip.

FIG. 21.—Origin of procambial strands in root as cells dividing only by axial walls; "initials" in resting condition, their nuclei having numerous nucleoli.

FIG. 22.—Later stage of cotyledons with procambial strands appearing; stem tip in resting condition.

FIG. 23.—Differentiation of stem tip, procambial strands, cortex, and epidermis.

IRON SUPPLY IN A NUTRIENT MEDIUM[1]

H. S. Reed and A. R. C. Haas

It has long been known that most plants become chlorotic when the nutrient medium is deficient in soluble iron salts. The problem of a suitable iron supply, although of great importance in artificial cultures, has never been solved satisfactorily. The composition of many nutrient solutions is such that soluble salts of iron cannot remain in solution for more than a brief period of time. Investigators have sought to meet the problem by frequent renewals of the solution, or by frequent additions of iron salts. The earlier workers generally employed inorganic salts of iron, but recent workers have also employed organic combinations, such as the citrate or tartrate. The "soluble ferric phosphate" seems to be a very satisfactory form of iron for water cultures. Duggar (3) pointed out that this material seems to give a colloidal solution of high dispersity and high stability, even in the presence of other salts. The possible significance of the colloidal state of nutrient salts for plants has recently been suggested by Comber (1).

In the course of an investigation on the growth of citrus trees and their absorption of materials from nutrient solutions, numerous cases of chlorosis appeared from time to time, despite the fact that special attention was given to the supply of iron salts. Not all cases of chlorosis in the trees could be correlated with an insufficient supply of iron. They often appeared to be connected with nutritional disturbances due to the absence of other nutrient ions. For example, when orange trees were grown in sand cultures receiving a potassium-free solution, incipient chlorosis appeared in the young leaves, but later the normal green color developed. Trees grown in sand cultures receiving a magnesium-free solution developed another type of chlorosis, which spread from a narrow strip along the midrib of the leaves until a considerable portion of the area was affected. Garner (4) has shown that certain types of chlorosis

[1] Paper no. 104, University of California, Graduate School of Tropical Agriculture and Citrus Experiment Station, Riverside, Cal.

in tobacco may be due to a deficiency of magnesium or of potassium. MILLER (11) and others have observed chlorosis of lemon leaves, which was due to a peculiar physiological condition of the trees, caused by the growth of adventitious roots. When lemons have been budded on sour stocks it sometimes happens that roots will grow from the base of the lemon trunk, just above the bud union. In such cases the branches directly above these adventitious roots usually bear chlorotic leaves. Recovery of these leaves follows the amputation of the root. The relation between the adventitious roots and the chlorotic leaves is not understood.

The relation of iron to chlorosis in citrus trees is not so certain as one might conclude from a hasty survey of the problem, although there are many cases in which the lack of iron is unquestionably the causal factor. Chlorosis may appear in citrus trees in the field, when the roots come in contact with a large excess of calcium and magnesium carbonates, or a large excess of sodium and potassium carbonates (LIPMAN 9).

Whether or not the chlorosis on the two types of abnormal soils is identical in nature, it is difficult to say with finality. There are certain differences in the appearance of trees and foliage between the two cases which counsel caution in rendering a decision on the point in question, and yet, in general, the disease seems to be the same.

From analytical data of soil extracts from normal and corral soils, LIPMAN reports that the extract of the normal soil was higher than that of the corral soil in total solids, volatile solids, non-volatile solids, nitrates, calcium, and magnesium, but that the reverse was true for phosphorus, potassium, and sodium. The OH-ion concentration of the corral soil was high, and no soluble iron was found below the first 8 inches of soil in either case. LIPMAN is of the opinion that a lack of usable iron for the normal functioning of the chlorophyll in citrus leaves still seems the best explanation for the cause of citrus chlorosis, although certain aspects of the question are obscure.

GILE and CARRERO (7) have shown that for rice plants neither increased calcium assimilation nor mere alkalinity is the primary cause of chlorosis, but that it is the insolubility of iron brought about by these secondary factors. GILE (5) analyzed pineapple

plants grown in soils high and low in calcium carbonate, and found that the chlorotic plants on calcareous soils contained more calcium and less iron in the ash, the other differences being slight or inconstant. He also found that the alkalinity induced by increasing amounts of sodium carbonate greatly depressed the growth without affecting the color of the plants.

McCALL and HAAG (**10**) have reported chlorosis in wheat plants in sand cultures when grown at different P_H values ranging from P_H 4.02 to P_H 7.0. VAN ALSTINE (**14**) found slight chlorosis in plants grown in solutions having a P_H value of 4.1. HOAGLAND (**8**) has emphasized the necessity of soluble iron in culture solutions, and has pointed out that the presence of sufficient dissolved iron in the culture solution will depend upon the form and quantity of the iron salt used, upon the concentration and reaction of the solution, and upon the length of time of standing. TOTTINGHAM and RANKIN (**13**) have shown that ferric citrate is a better source of iron for wheat seedlings than ferric sulphate, ferrous sulphate, or ferric phosphate, and possesses a fair degree of solubility over a considerable range of P_H value of the nutrient solution. The variation in efficiency of iron in the different forms supplied is correlated with variation either in the solubility of this element or in the modification of the P_H value of the nutrient solution.

It was with a view to determining some of the conditions which affect the amount of soluble iron salts in nutrient solutions that the following studies were undertaken. The problem is one of considerable importance for the intelligent use of nutrient solutions.

Effect of reaction upon amount of iron in solution

The solution designated as Hoagland's nutrient solution has been successfully employed in the experimental cultures of citrus trees and other plants. It contains 1455.1 parts per million of salts. Its composition is shown in table I in the column designated "1–5." The reaction of the freshly prepared solution was P_H 5.2. The other solutions whose compositions are given in table I are modifications of Hoagland's solution.

Tests were made to determine what changes in the solubility of iron salts occur in two types of nutrient solution used in experiments with young citrus trees. A set of ten flasks, each holding

one liter of Hoagland's nutrient solution, was prepared in such a way that they contained from 5 to 25 parts per million Fe (table II). Five of the flasks were given 300 gm. of pure silica sand and shaken.

TABLE I

COMPOSITION OF NUTRIENT SOLUTIONS

Series	1–5 (p.p.m.)	30–35 (p.p.m.)	36–41 (p.p.m.)
Fe	1	1	1
Mn	0.1	0.1	0.1
Ca	159	.....	159
Mg	54	54	54
K	185	496	496
Na	7	280	280
PO_4	105	105	105
SO_4	216	214	214
Cl	10	10	291
HCO_3	.....	725	725
NO_3	718	718	718
Total concentration	1455.1	2603.1	3043.1

TABLE II

CHANGES IN SOLUBILITY OF IRON SALTS IN CULTURE SOLUTIONS

Culture solution	Number of days before making tests	Parts per million of Fe supplied				
		5	10	15	20	25
		Parts per million of Fe found				
Hoagland's	1	0.5	1.0	1.5	1.7	2.0
Hoagland's	8	0.4	0.5	0.8	1.1	1.3
Hoagland's plus sand	1	0.5	1.0	1.5	1.7	2.0
Hoagland's plus sand	8	0.1	0.1	0.1	0.2	0.5
Hoagland's without Ca, plus $NaHCO_3$	2	0.2	0.3	0.5	0.8	1.0
Hoagland's without Ca, plus $NaHCO_3$	28	0.2	0.2	0.2	0.2	0.2
Hoagland's without Ca, plus $NaHCO_3$ plus sand	2	0.2	0.3	0.5	0.8	1.0
Hoagland's without Ca, plus $NaHCO_3$ plus sand	28	0.2	0.2	0.2	0.2	0.2

Another set of ten flasks was prepared in the same way as the first except that the solution was modified by the addition of 1000 parts per million of sodium bicarbonate, with calcium omitted entirely (table I, column "30–35"). The modified solution had a P_H of 7.5. Table II shows the rapid reduction in the amount of soluble

iron remaining in the solution, even when the initial concentrations were quite high. At the end of one day the amounts of dissolved iron in the flasks of Hoagland's solution depended upon the amounts originally supplied, the presence of sand having no effect. At the end of eight days, however, the flasks containing sand contained appreciably less soluble iron than those without sand. The rate at which iron disappeared from solution in the flasks containing sodium bicarbonate seems to be independent of the presence of sand.

The results presented in table II show how rapidly soluble iron salts disappear, even from a solution having an initial P_H of 5.2. At the end of one day approximately one-tenth of the iron added was still in soluble form. The amount of soluble iron is more quickly and completely reduced in solutions of increased alkalinity. These results emphasize the necessity for maintaining the supply of soluble iron by the renewal of the solutions or by the addition of iron salts at frequent intervals. A very small amount is doubtless adequate if the supply is maintained.

This whole problem has received elucidation from the work of PATTEN and MAINS (12), who have determined the H-ion concentration at which iron is precipitated from hydrochloric acid solutions by various alkalies. They found that if hydroxide is added to a dilute solution of ferric chloride, ferric hydroxide is formed if the mixture has a P_H value of 3.5. A faint cloudiness was apparent at P_H 3.5, which increased to a fine precipitate at P_H 5.5, becoming very heavy at P_H 6.0. Since it appears that iron salts become almost entirely insoluble, it becomes of interest to see what happens when the P_H of the solution is lowered by the introduction of CO_2. It is known that growing roots evolve measurable quantities of CO_2, and it has been suggested that the CO_2 evolved by plant roots is an important factor in bringing into solution otherwise insoluble iron compounds in these soils.

The following experiment was designed to throw some light upon the efficiency of CO_2 as a solvent for iron in solutions. Hoagland's solution was supplied with approximately 75 parts per million of Fe in the form of ferric tartrate and left over night. On the following morning a filtered portion of the solution contained

8 parts per million of soluble Fe. A stream of CO_2 was then passed through the unfiltered solution for several hours. At the end of that time the P_H and Fe content of a filtered portion of the solution were found to be the same as before the CO_2 was introduced. It appears that CO_2 is not able to change appreciably the reaction of a solution which had an original P_H of approximately 5.0, hence we should not expect it to increase the solubility of iron by virtue of its acid properties. The results were somewhat different when solutions of a higher P_H were employed. Culture solutions containing sodium bicarbonate were studied in a similar manner. Solution 30–35 (table I) which contained no calcium, and solution 36–41 which contained calcium, had P_H values of 7.5. Each solution received approximately 75 parts per million of Fe in the form of ferric tartrate and a small amount of solid ferric phosphate. After two hours there was no soluble Fe remaining in either solution. After the addition of another small quantity of ferric tartrate the solutions were left standing over night. On the following morning no soluble iron was found in filtered portions of either solution. A stream of CO_2 was led through each of the turbid solutions for several hours. When it was discontinued, portions of the solutions were filtered and their P_H and Fe contents at once determined. The P_H of both solutions had been changed from 7.5 to approximately 6.0, but there was no trace of soluble iron demonstrable by the colorimetric method employed.

While the introduction of CO_2 changed the reaction of the solutions, it did not increase the amount of soluble iron. In the separation of the members of the Fe-Al-Cr group in qualitative analysis, many organic substances prevent or interfere with the precipitation of iron by ammonium hydroxide. The effect of organic matter on the uptake of iron from calcareous soils is explained by COMBER (1) as being due to the solvent action of many organic compounds upon iron salts over a wide range of both acid and alkaline reactions. GILE and CARRERO (6) found that ferric citrate furnished sufficient iron for the growth of rice in either acid or neutral solutions, but that ferric tartrate furnished sufficient iron when added to alkaline solutions. As a result of their investigations it was found that these organic compounds of iron are non-toxic at the concentrations

they employed. Table III summarizes the results obtained when various organic compounds were added to the nutrient solution. The culture solution "36–41" (table I) was used and had a P_H of approximately 7.5. Abundant ferric tartrate solution was added, but soon a copious precipitate settled out, and after standing over night, less than 1 part per million of iron still remained in solution. The solution was shaken and portions of the turbid solution were added to several flasks. Various organic compounds were added to the flasks, one flask being retained as a control. The flasks were then left standing a few hours. The results, while only qualitative, give a good idea of the relative amounts of iron in the filtrates after a short time interval. The object of the tests was to show the effects of various organic compounds on the solubility of iron, irrespective of their effects upon plant growth. Certain of the compounds could not be used in nutrient solutions because of their toxicity.

By supplementing the potassium sulpho-cyanide method with potassium ferrocyanide tests, it was found that glucose, sucrose, glycerine, starch, and sodium acetate each caused slightly increased solubility of iron. The filtrate from the nutrient solution which contained sodium potassium tartrate gave a deep yellow when the potassium thiocyanate method was employed in the normal manner. When the order of adding the reagents to the glass comparison tube was reversed, that is, by gradually adding the test solution to the thiocyanate and sulphuric acid, a distinct deep red was developed which almost immediately broke down to a deep yellow. When this method was employed with the filtrate from the nutrient solution treated with potassium oxalate, no red color was observed. Possibly here the decomposition of the red solution may have proceeded too rapidly to be detected. Upon adding the sodium salicylate to the nutrient solution, a clear, deep wine-red color was obtained. The conspicuous color of the iron compound thus formed has been suggested recently by COMBER (2) as a test for "acid soils."

Table III makes it evident that ammonium salts of organic acids, while they increase the solubility of iron compounds, greatly decrease the P_H of the solution. It seemed possible that the

increased solubility of the iron in such cases was due largely to the decrease in P_H. Accordingly, sodium or potassium salts of organic acids were used, with the result that citrates and tartrates effected

TABLE III

EFFECT OF ORGANIC SUBSTANCES ON SOLUBILITY OF IRON IN NUTRIENT SOLUTIONS (SOLUTION 36–41)

Compound added	Appearance of contents	Color of filtered solution	Approximate P_H after adding compound and filtering nutrient solution	KSCN test for iron in filtrate
Control	Turbid (sediment)	Colorless	7.6	None
Sodium acetate	Turbid (sediment)	Colorless	7.6	Trace
Ammonium citrate	Clear	Yellow	<4.5	Abundant
Sodium salicylate	Clear	Wine-red	7.6	Abundant
Ammonium tartrate	Clear (traces of sediment; no turbidity)	Yellow	<4.5	Abundant
Glycerine	Turbid	Faintly yellow	7.6	Trace
Gelatin	Turbid	Faintly yellow	7.6	Trace
Soluble starch	Turbid	Yellowish brown	7.0–7.4	Deep yellow-brown, clear; Fe present by ferro-cyanide test
Sucrose	Turbid	Faintly yellow	7.6	Trace
Dextrose	Turbid	Yellowish	7.6	Trace
Glue	Turbid	Faintly yellow	7.6	Trace
Sodium citrate	Fine turbidity	White finely divided turbidity when filtered through filter paper; clear when filtered through Chamberland filter	7.6	Abundant
Potassium oxalate	Turbid, some sediment	Colorless	6–6.5	Yellow; reversing order of reagents still gave yellow color
Sodium potassium tartrate	Clear	Colorless	7.6	Deep yellow; when reagents were reversed deep red obtained for moment, at once breaking down to yellow

marked solubility of iron without altering appreciably the P_H of the solution. Sodium acetate failed to cause an appreciable increase of dissolved iron with the tests applied, although the organic matter was destroyed before making the test. The organic compounds such as starch, sugars, etc., although not increasing very markedly the solubility of iron, nevertheless dissolved appreciable amounts of it. This is of considerable importance because a very low maintained concentration of dissolved iron is adequate for plant nutrition.

Summary

1. The iron of ferric tartrate soon becomes converted into insoluble compounds when added to nutrient solutions, and the change is more rapid in solutions of higher P_H.

2. The introduction of carbon dioxide lowers the P_H of slightly acid, neutral, or alkaline solutions, but does not increase the solubility of iron compounds which they contain.

3. The addition of certain organic compounds to an alkaline nutrient solution increases the amount of soluble iron in the solution. This fact may be of significance in maintaining an adequate supply of soluble iron in solutions for the growth of plants.

CITRUS EXPERIMENT STATION
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LIFE HISTORY OF ENCEPHALARTOS

CONTRIBUTIONS FROM THE HULL BOTANICAL LABORATORY **316**

PAUL J. SEDGWICK

(WITH PLATES XXI, XXII AND FOUR FIGURES)

With the exception of *Bowenia*, less is known and has been published concerning the life history of *Encephalartos* than any other member of the Cycadales. In 1910 SAXTON (**13**) published the only morphological paper dealing solely with this genus, an account of the later embryogeny in *Encephalartos Friderici Guilielmi* and *E. villosus*. CHAMBERLAIN has made frequent incidental reference to *Encephalartos* in his various papers on other cycads, and PEARSON (**12**) has given valuable field descriptions in his *Notes on South African cycads*, in which he discusses three species of the genus. Before his death, PEARSON had in preparation another paper under the same title which was never completed. His notes for this paper were very kindly furnished me by Miss STEVENS of the University of Cape Town, and some further reference will be made to them. PEARSON had also contemplated an investigation of the life history, but this was not completed. CHAMBERLAIN (**6**) also has studied *Encephalartos* in the field. Miss SMITH (**14**) has estimated the number of sporangia borne on a microsporophyll of *E. villosus* as 500; and in *E. Caffer* as 700. She also gave a description of the mature microsporophylls of *E. villosus*, *E. Caffer*, and *E. Altensteinii*.

The purpose of this investigation was to establish the life history of *Encephalartos* as completely as its inaccessibility and the difficulty of securing material would permit. It was especially desired to obtain the early proembryo stages, and thus complete, with SAXTON's account of the later embryogeny, the embryogeny of *Encephalartos;* and to attempt to use this account in a phylogenetic comparison with other cycads. It was also hoped that the male gametophyte might be studied in close enough detail to permit the making of a phylogenetic comparison, but this latter hope was not fulfilled, owing to a scarcity of available stages.

Materials and methods

The material for this investigation was procured from a number of sources. Much of it was collected by CHAMBERLAIN during his visit to South Africa in 1912. He collected material of *Encephalartos Altensteinii*, *E. Friderici Guilielmi*, and *E. villosus*. Professor WORSDELL supplied a young staminate cone of *E. brachyphyllus*. Miss STEVENS sent a box of PEARSON'S slides of *E. Altensteinii*. Miss VAN ROOYEN furnished most of the material of *E. villosus* from Kentani, Transkei, South Africa. Additional material has come from the botanical garden of the University of Chicago, from Fairmount Park in Philadelphia, and from the botanical garden at Bonn, Germany. All of the material came into my possession through the kindness of Professor CHAMBERLAIN, to whom I am greatly indebted for many suggestions during the progress of the work.

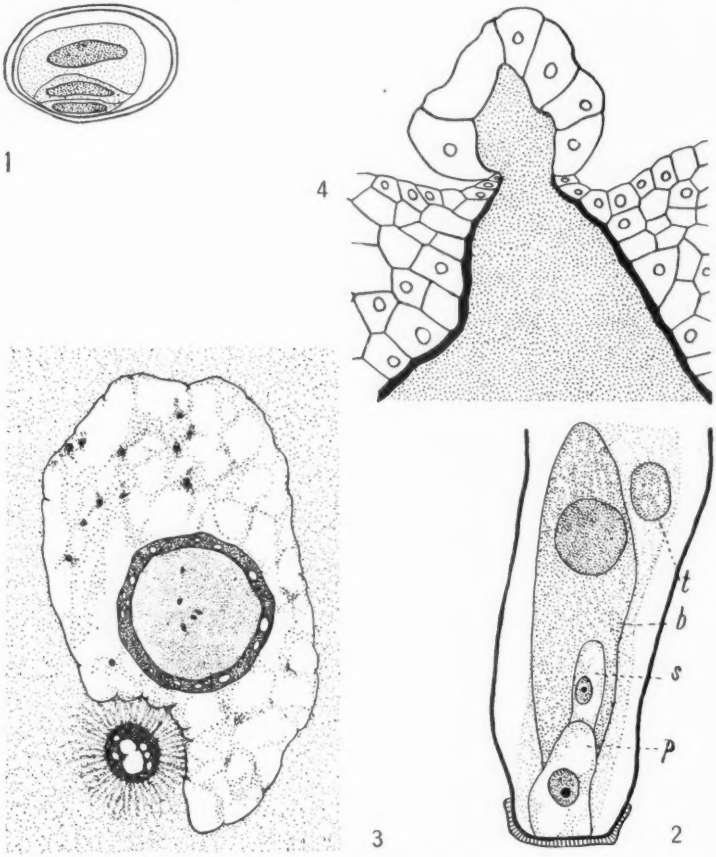
Sections were made 3–12 μ in thickness with a Spencer rotary microtome, and stained in iron-alum haematoxylin with a light background of gold orange. It was found that the archegonium and proembryo could best be handled in sections 8–10 μ in thickness, while pollen grains were best sectioned at 3 μ.

Male gametophyte

At the time of the shedding of the pollen, the male gametophyte is in the usual three-celled condition. Later stages seem to be rare (fig. 1). In PEARSON'S slides of *E. Altensteinii* several later stages were found, but none of them was sufficiently advanced to show sperms or sperm mother cells. In this material the earliest stage shows the gametophyte of four cells, the vegetative, stalk, body, and tube cells. The haustorial portion of the pollen tube has commenced invasion of the nucellus. The prothallial, stalk, and body cells are in a line just as in *Dioon*, *Zamia*, and *Ceratozamia*. The prothallial cell bulges into the stalk cell very slightly, but the prothallial and stalk cells together press very deeply into the body cell (fig. 2).

In later stages the pollen tube is found penetrating the nucellus, but in no case was it seen to branch. The blepharoplasts have now appeared in the body cell, and from the few cases observed it is evi-

dent that the blepharoplasts appear first in the fore and aft position, and later swing through 90°, coming into a position transverse to



FIGS. 1–4.—Fig. 1, *E. villosus:* three-celled gametophyte in pollen grain; ×996; fig. 2, *E. Altensteinii:* gametophyte of four cells, prothallial (*p*), stalk (*s*), body (*b*), and tube (*t*); ×270; fig. 3, *E. Altensteinii:* detail of body cell nucleus and blepharoplast; ×996; fig. 4, *E. villosus:* archegonium with more than two neck cells (very common condition in this species), cells evidently arising from continued division of two original neck cells; ×225.

the long axis of the tube. A detail of the nucleus of the body cell and one of the blepharoplasts is shown in fig. 3. The second ble-

pharoplast is not present in this particular section. The blepharoplasts with their radiations are imbedded or pressed into pockets in the nuclear membrane, the appearance almost suggesting that the rays had beaten in the membrane. Later stages were not found, but the presence and position of the blepharoplasts indicate that division of the body cell is close at hand, and that two sperms will be formed.

Female gametophyte

The megaspore, the first cell of the female gametophyte, has been observed in only three of the nine genera of cycads. In *Stangeria paradoxa*, LANG (**11**), and in *Ceratozamia longifolia*, TREUB (**17**), describe an axial row of three "megaspores," of which the innermost one is functional. In *Zamia floridana*, Miss SMITH (**15**) figures an axial row of four megaspores, the innermost one functioning. In the cycads it is exceedingly difficult to obtain such early stages, because the young cones are completely concealed by the bud scales, and it is impossible to determine from superficial examination whether the bud contains a cone, or only a new crown of leaves.

In the present material the earliest stage available shows free nuclear division of the gametophyte. The ovules from which the sections were made had been pickled whole, and the gametophytes had shrunken away from the periphery of their cavities. The approximate dimensions of the cavity are 22.5 mm. × 12 mm. The layer of cytoplasm containing the imbedded nuclei is very thin in proportion to the huge vacuole, being 50μ thick. The nuclei are in one layer. While the gametophyte is still in an early free nuclear condition, organization of the pollen chamber is indicated in the nucellus above the gametophyte. The pollen chamber appears first as a region in the central portion of the nucellus, well below the nucellar beak, where the cells in a vertical line are becoming separated from their neighbors through middle lamella resorption (fig. 14).

Early stages of wall formation in the gametophyte have not been found, the next stage showing the nearly mature gametophyte with central cells nearing the time for division. In these archegonia the primary neck cell has already divided to form the two neck cells.

Occasionally the two neck cells divide, giving rise to several cells, as shown in fig. 4. It is possible in numerous instances to observe the behavior of the central cell nucleus in preparation for division. At the time when radiations in the cytoplasm are lining up and attaching themselves to the nuclear membrane, showing clearly that division is imminent, the central cell nucleus is very large in proportion to the contained chromatin and other material (fig. 7). The nucleus seems to have a topography resembling that of a nucleus in synapsis, and the contracted appearance, as in synapsis, is due largely to a rapid increase in the size of the nuclear cavity, rather than to any contraction of the chromatin. Most of the nuclear cavity is filled with a homogeneous plasm and ten or a dozen roughly spherical, light staining bodies with dark centers. The chromatin and another material (for it does not seem probable that the great quantity of darkly staining material is all chromatin) are in a close spirem. That not all of this material is chromatin is shown by a study of the figure for the division of the central cell. Until earlier stages were located this topography was puzzling. In the younger central cell nucleus there is no such disproportion between the volume of the whole nucleus and the volume of contained chromatin and other undetermined darkly staining material. The volume of the nucleus increases by a peculiar engulfing of general cytoplasm, the nuclear membrane bulging inward. Later the membrane heals over and the engulfed membrane must be resorbed, dissolved, or otherwise disappear. Furthermore, it seems that certain food bodies which are found to be abundant in the cytoplasm of the central cell are taken into the nucleus in the same manner, and these are the roughly spherical, dark centered bodies previously mentioned. The process bears a very close resemblance to the behavior of the male and female nuclei of *Peperomia* in the absorption of protoplasm, as described by BROWN (1). The occasion for this great growth of the central cell nucleus is not understood (figs. 5–7).

As already mentioned, the central cell nucleus, which so resembles a nucleus in synapsis, has already begun to show radiations in the cytoplasm, indicative of its early division. Details of the division were not observed, the next stage found showing the egg nucleus and ventral canal nucleus at telophase, with membranes forming.

Prominent spindle fibers connect the nuclei, and polar radiations are very distinct. There is no evidence of even an evanescent accumulation of wall material on the spindle fibers. Thus *Encephalartos* is similar in this respect to all the cycads so far studied. In the division observed, the ventral canal nucleus was considerably smaller than the egg nucleus, seeming to indicate that it would very shortly degenerate. Either this was not a normal division, or this assumption is incorrect, because in most cases the ventral canal nucleus was not observed to degenerate promptly, as is usually the case in cycads. Instead, the ventral canal nucleus enlarges rapidly and seems to go through a maturation phase similar to that of the egg (figs. 8, 9). Here again there is some evidence that the ventral canal nucleus grows by the amoeba-like intake of food and protoplasm described for the central cell nucleus, instead of simply by osmotic absorption, as must naturally be assumed in the absence of such a condition. In the case of the ventral canal nucleus growth, however, available stages are not so good as the stages showing the growth of the central cell nucleus.

Embryogeny

Fertilization was not observed, and apparently fertilization by a sperm is not necessary in *Encephalartos* for the successful development of embryos. In greenhouse material and material collected in the field it is found that the ventral canal nucleus, instead of degenerating, has enlarged and is approaching the egg. The first case of fertilization described for gymnosperms by STRASBURGER (**16**) for *Picea*, and the second case, described for *Pinus* by COULTER (**7**), were of this character (figs. 8, 9). CHAMBERLAIN (**3**) has reported a similar condition as occurring occasionally in *Ceratozamia* and *Encephalartos*. He concludes that a union of the two nuclei is very probable. The present observations support this conclusion. While the two nuclei were not actually found in union, they were very close together. In his paper on *Ceratozamia mexicana*, CHAMBERLAIN (**3**) believes that this situation throws an explanatory light on VAN TIEGHEM's reported hybrids, a cross between *C. longifolia* and *C. mexicana* in which three year old pollen of *C. mexicana* was used. It is not believed that cycad pollen will

live three years. CHAMBERLAIN thinks that either the ventral canal nucleus united with the egg nucleus, or that the embryo was produced without a union.

An additional reason for concluding that fertilization by a male nucleus may not be necessary is based on CHAMBERLAIN'S field observations. In collecting *Encephalartos Friderici Guilielmi*, during a whole day's search, with the aid of four assistants, he procured only one staminate cone in the neighborhood of plants bearing ovulate cones. A further reason for concluding that sperm fertilization is frequently lacking is found in careful study of all the preparations. In not a single free nuclear proembryo has a sperm sheath or ciliated band been found. In the studies previously made by LANG (11) and CHAMBERLAIN (2) it is reported that the sperm sheath and the ciliated band persist in the cytoplasm of the cycad proembryo up to a very late stage of free nuclear division, and often even after cell walls have begun to appear. The cytoplasmic sheath of the sperm, and especially its ciliated spiral band, are so conspicuous that failure to find them in complete serial sections is practically a proof that they are not present. In view of these three considerations, therefore, it is safe to conclude that *E. villosus* and *E. Friderici Guilielmi* can produce normal embryos in the absence of pollination and fertilization by a sperm. This does not mean that sperm fertilization never takes place, but simply that the preparations examined do not show any indication of sperm fertilization, and they do show proembryos and embryos which seem to be normal. PEARSON (12 and unpublished notes) thought it probable that *E. villosus* is insect pollinated, since the coming specimens were frequently so situated that it is unreasonable to suppose that wind could carry the pollen and deposit it in sufficient quantity to account for the numerous embryos. Furthermore, he found certain species of the weevil, *Phaeophagus*, constantly associated with the cones, and the bodies of the weevils are frequently smeared with pollen. There is also similar evidence for belief that *E. Friderici Guilielmi* and *E. Altensteinii* may be insect pollinated. Observations showing that fertilization is not necessary would permit that coming specimens be isolated, and thus make it unnecessary to search for insect pollination. It is very possible, however, that when normal pollination and fertilization

occur, the pollen may be carried as suggested by PEARSON. CHAMBERLAIN, however, believes that there is no insect pollination in any of the cycads.

The earliest free nuclear divisions of the proembryo were not observed. The latest free nuclear stage found seemed to have a fairly close approximation to the 1024 nuclei which would result from the tenth simultaneous division (fig. 11). Neither in this stage nor in any of the preceding stages was an evanescent segmentation, such as CHAMBERLAIN (**2, 5**) describes for *Stangeria* and *Dioon edule*, observed. Since the division figures were not found, it is impossible to say whether such an evanescent segmentation occurred. It is possible to conclude that since there is no segmentation with the nuclei of the tenth division in the resting condition, either another division will take place or cell walls are not formed in the usual manner.

When next observed, the proembryo is made up of cellular tissue, with definite permanent cellulose walls. The suspensor has started to elongate and differentiation of the embryo has begun. There is some indication of the breaking down of the cellular tissues at the center of the proembryo (figs. 12, 13). The next stages show the elongating suspensor, twisted in the embryo cavity and now backing up into the empty archegonium. The development of the embryo proper has been described by SAXTON (**13**), and will not be taken up here, except to remark that the cotyledons and stem tip can be distinguished in the present material considerably earlier than in any figured by SAXTON. His earliest stage shows the proembryonal tissue completely broken down, while this material shows a differentiation of cotyledons and stem tip before the proembryonal tissue has completely disorganized.

It is interesting and suggestive to compare the embryogeny of *Encephalartos* with the embryogeny of other cycads. *Cycas*, *Zamia*, *Ceratozamia*, *Dioon*, *Stangeria*, and *Macrozamia* have been investigated, *Zamia* and *Stangeria* receiving the more thorough attention. In *Macrozamia Moorei* and *E. Friderici Guilielmi* segmentation is complete and permanent, cellulose walls being formed throughout the proembryo. Later a cavity forms by the breaking down of the cellular tissue. COULTER and CHAMBERLAIN (**9**) believe, from examination of the figures on *Cycas* by IKENO (**10**) and TREUB, and from

slides made from material furnished by IKENO, that segmentation is also complete in *Cycas*. If this is correct, it follows that the figures given by IKENO and TREUB are of rather an advanced stage in the breaking down of the cellular tissue. In *Dioon edule* and *Stangeria paradoxa*, evanescent walls appear throughout the entire proembryo, but permanent walls are formed only at the base. In *Zamia floridana*, COULTER and CHAMBERLAIN (**8**) found that segmentation takes place only at the base. *Bowenia* and *Microcycas* have not been investigated. The question naturally arises as to whether the development of the proembryo shows any evolutionary significance. It is generally agreed that *Cycas* is the most primitive living cycad, this conclusion being based largely on the leafy character of the ovulate sporophyll, and the absence of a definitely organized ovulate strobilus. *Macrozamia Moorei* is also accorded a primitive position, on the basis of an entirely different character, namely, the possession of numerous lateral cones, and, associated with this condition, the absence of cone domes. Furthermore, the leaf trace is direct. *Encephalartos*, like *Macrozamia*, possesses numerous lateral cones, but by no means so great a number. Thus there is evidence for primitiveness in *Encephalartos* just as in *Macrozamia*. On the other hand, it has long been agreed that *Zamia* is the most advanced of the cycads. Its compact cones, the practically entire loss of leaflike character of sporophylls, the reduced number of microsporangia, the girdle of leaf traces, and the possession of cone domes, all testify to the advanced position of *Zamia*. So the evolutionary series, based on external characters and gross morphology, runs from *Cycas* through *Macrozamia*, *Encephalartos*, *Stangeria*, and *Dioon* to *Zamia*, and a study of the embryogeny provides a distinct confirmation. In the primitive genera the proembryo becomes completely cellular (*Encephalartos*, *Macrozamia*, and *Cycas*); the next stage in evolution is where segmentation is evanescent except at the base from which suspensor and embryo are organized (*Dioon*, *Stangeria*); while in the final stage, as shown by *Zamia*, segmentation never takes place except at the base. It will be interesting to learn the embryogeny of *Microcycas* and *Bowenia*. If this theory of the evolution of the embryogeny is correct, we should expect *Bowenia* to show complete segmentation with walls, perhaps permanent, but more probably evanescent.

Microcycas presents such a mixture of advanced and primitive characters that it would be entirely unsafe to guess at its embryogeny. Cycad embryogeny from an evolutionary standpoint has been discussed by CHAMBERLAIN (**6**).

Summary

1. An extensive free nuclear period follows the germination of the megaspore.

2. The pollen chamber begins to form within the nucellus while the gametophyte is still in an early free nuclear stage. It appears first in the central portion of the nucellus below the nucellar beak.

3. The male gametophyte has prothallial, stalk, body, and tube cells. The body cell was observed with two prominent blepharoplasts. The pollen tube is unbranched.

4. The central cell nucleus enlarges greatly before its division to form the ventral canal and egg nuclei. Increase in the volume of the nucleus takes place by the bodily inclusion of masses of cytoplasm.

5. The ventral canal nucleus frequently does not promptly degenerate, but enlarges, goes through a period of maturation very similar to that of the egg, and passes toward the egg, suggesting a probability of fusion of egg and ventral canal nuclei.

6. No proembryos were found containing sperm remnants, indicating that fertilization by a sperm is not necessary for the production of the proembryo.

7. The 1024-nucleate stage of the proembryo shows neither walls nor evanescent segmentation. Evanescent segmentation may have occurred following this tenth division, but its disappearance or its failure to appear, whichever is true, indicates that another division is to take place.

8. The proembryo becomes completely cellular. Later a vacuole forms by the breaking down of the central portion of the proembryonal tissue; eventually this tissue is completely resorbed.

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EXPLANATION OF PLATES XXI, XXII

FIG. 5.—*Encephalartos villosus:* central cell nucleus taking in cytoplasm; pore not yet closed over; ×251.

FIG. 6.—*E. villosus:* central cell nucleus taking in cytoplasm; ×251.

FIG. 7.—*E. villosus:* central cell nucleus shortly before division; ×324.

FIG. 8.—*E. villosus:* ventral canal nucleus enlarging and moving toward egg nucleus; ×32.

FIG. 9.—*E. villosus:* ventral canal nucleus moving toward egg nucleus; ×32.

FIG. 10.—*E. villosus:* an unusual archegonium with very long neck region; ×80.

FIG. 11.—*E. Friderici Guilielmi:* free nuclear proembryo (approximately 1024 nuclei at this stage); ×26.

FIG. 12.—*E. Friderici Guilielmi:* cellular proembryo; vacuole forming at center through breaking down of cells; ×69.

FIG. 13.—*E. Friderici Guilielmi:* suspensor and embryonal region; from same section as fig. 12; ×69.

FIG. 14.—*E. brachyphyllus:* origin of pollen chamber through disorganization of cells in central portion of nucellus; at this time gametophyte is in early free nuclear condition; ×50.

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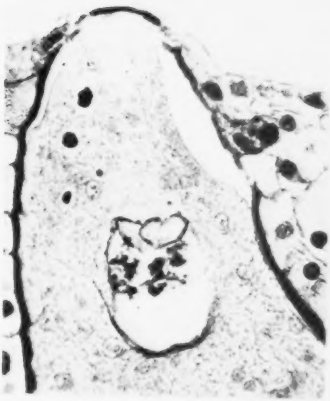

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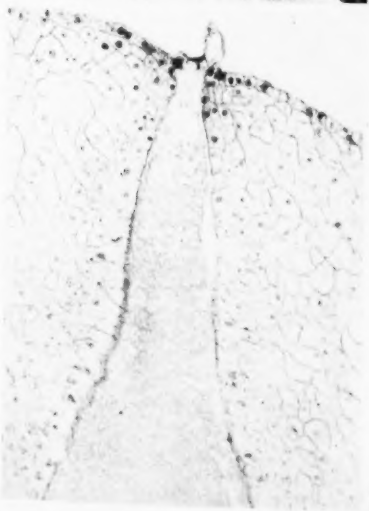

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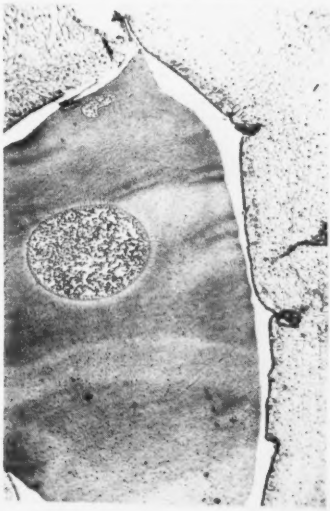

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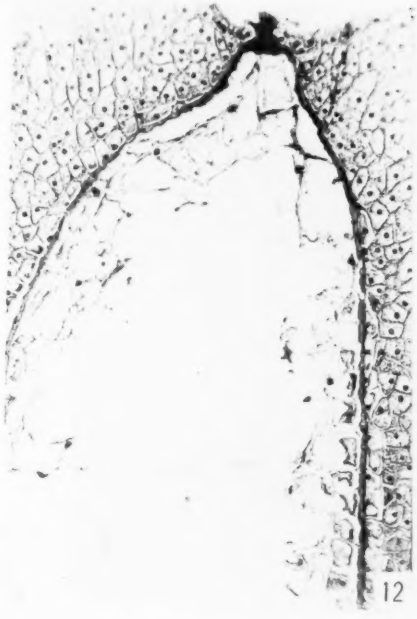
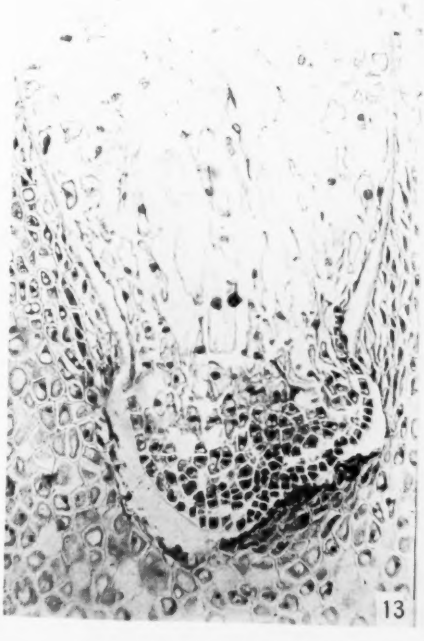
SEDGWICK on ENCEPHALARTOS





SEDGWICK on ENCEPHALARTOS

ASSIMILATION-RESPIRATION BALANCE AS RELATED TO LENGTH OF DAY REACTIONS OF SOY BEANS

FRANK M. EATON

(WITH FOUR FIGURES)

Considerable interest has recently been directed toward the seasonal behavior of plants by the work of GARNER and ALLARD.[1] These investigators have laid particular stress upon the relative length of day and night as the factor which directs plant growth to the vegetative and reproductive stages. Later HARVEY[2] has shown that a wide range of plants may be brought to sexual maturity under conditions of uniform temperature and continuous artificial light. HOPKINS,[3] in his statement of the bioclimatic law, would include besides length of day (latitude) all of those climatic factors which are influenced by longitude and altitude. It is doubtless true in nature that the seasonal changes in the development of vegetative and reproductive characters correspond most closely to changes in the relative length of day and night. One of the chief functions of a plant peculiar to the hours of daylight is the assimilation of carbon dioxide. In the absence of light this process is found measurably reversed through respiration.

The somewhat preliminary experiments to be described here were planned with a view toward finding whether the daily balance between these two plant processes, assimilation and respiration, might not stand as a controlling influence which could direct plant growth either to a vegetative or reproductive form. If this were the case, then it would be expected that lower daily temperatures, increased nightly temperatures, or a reduction in the number of hours of the day during which carbon dioxide was available for assimilation would bring about changes in the behavior of plants similar to those which follow a decrease in the length of day.

[1] GARNER, W. W., and ALLARD, H. A., Jour. Agric. Res. **18**:553–606. 1920.

[2] HARVEY, R. B., Growth of plants in artificial light. BOT. GAZ. **74**:447–451. 1922.

[3] HOPKINS, A. D., Periodic events and natural law as guides to agriculture research and practice. Monthly Weather Review Suppl. no. 9. 1918.

Nightly temperatures can be controlled experimentally with comparative ease and with little disturbance of the other external factors upon which plant growth is dependent. This method was used first and most extensively. Later, as a check upon the results so obtained, a few plants of Peking soy beans were deprived of carbon dioxide for a number of the hours of the day. Soy beans were used as a principal test plant because GARNER and ALLARD had already so thoroughly demonstrated their length of day responses.

Effect of different nightly temperatures upon time of flowering of Peking soy beans

Three sets of twelve plants of Peking soy beans were given a thirteen-hour day out of doors. During the nights one set of these was placed in a chamber with a temperature of about 50° F., the second set in a control chamber at about 65°, and the third was given a nightly temperature of 90°.

TABLE I

PEKING SOY BEANS PLANTED JUNE 20 (SPROUTED SEED): UP JUNE 24; TREATMENT STARTED JUNE 20, 1922

	Cold	Check	Hot
Days from emergence to flowering	45.0	25.0	21.0
Unfolded leaves, 21st day (July 15)	6.0	6.2	7.3
Height (cm.)	7.7	8.6	8.6
Leaves, 45th day (August 8)	11.1	9.0	9.0
Height (cm.) 45th day (August 8)	32.0	25.0	28.0
Height (cm.) at maturity	60.0	25.0	28.0
Total dry weight, plant and beans	292.4	81.8	122.2

The differences in the time of flowering of these sets of plants were almost as great as the difference effected by GARNER and ALLARD by exposing plants to varied lengths of day. The set given the cold nights flowered on the forty-fifth day after germination, those in the check chamber on the twenty-fifth day, and those in the hot night chamber on the twenty-first day (fig. 1). Untreated plants grown in the field under a full day flowered three days earlier than did the plants given the cold nights, the latter receiving only the thirteen-hour day. The behavior of these plants is shown more completely in table I.

The soy beans used in this experiment were grown in wooden boxes four feet long and one foot square. They were placed on trucks and pushed into the respective temperature control chambers at 7 P.M. and removed each morning at 6 A.M. The temperature of the cold night chamber was reduced by circulating the air of the chamber through an ice chest filled with cracked ice. The temperature of the check chamber was uncontrolled. Electric heating elements with thermostatic control and a circulating fan were used for heating the hot chamber.

FIG. 1.—Peking soy beans, showing effect of hot and cold nights upon growth

MEASUREMENTS OF ASSIMILATION AND RESPIRATION.—As the foregoing results were quite outstanding, it seemed desirable that a quantitative estimate of the respiratory rates of the plants in the various chambers and the ratio of assimilation to respiration be secured. While time and equipment were not available for the development of elaborate technique, data of some interest were secured.

For the measurement of both assimilation and respiration, rooted plants were transplanted to trays four inches deep and one foot square. Over the top of these trays a heavy plate glass with

a ground surface was placed. In the center of each plate there was a one-inch hole through which the stalk of the plant extended. The space between the plant stalk and the edge of the opening was filled with wax, forming an air-tight seal between the soil below and the air above. While measurements were being made the plants were covered with bell jars which were sealed to the ground glass plate. In measuring respiration the plants were placed in the respective temperature chambers at 7 P.M. and removed the following morning at 6 A.M. From each of the bell jars there were two tubular openings connected with the outside of the chambers by rubber tubing. Before removing the plants at 6 A.M., the air in the bell jars, which then contained the additional CO_2 of respiration, was drawn off for a minimum period of one hour and passed through barium hydroxide bead towers, the barium hydroxide later being titrated with tenth normal hydrochloric acid. By estimate five volumes of air were removed from the bell jars for each determination. The air as removed was replaced with carbon dioxide free air. Assuming that each volume of air removed halved the CO_2 content of the bell jar, then one thirty-second of the CO_2 would still have remained, plus a portion of the carbon dioxide respired by the plant during the last hour. This error is not accounted for in the results, but the original CO_2 content of the normal air in the bell jar when the plant was covered has been subtracted.

The assimilation measurements were made out of doors with plants which had been used for respiration measurements. A stream of air, as nearly constant in its rate of flow as possible, was provided by means of a valve opening into a large vacuum tank connected to a motor-driven exhaust pump of sufficient size to maintain the partial pressure of 12 cm. mercury in the tank. For a fifty-minute period the air entering the valve was drawn from the bell jar containing the plant and passed through a barium hydroxide bead tower. For the succeeding ten-minute period normal air was drawn through a second bead tower. This alternating process was continued for a thirteen-hour day. The barium hydroxide of the respective bead towers was titrated and renewed at the end of each period. The CO_2 content of the normal air passing through

the bead tower for the ten-minute period was determined and multiplied by five. This value was taken as the equivalent of the CO_2 supplied to the plant during its fifty-minute period. The amount of CO_2 leaving the bell jar, subtracted from the amount which entered, gave the difference representing the CO_2 assimilated by the plant for one hour.

TABLE II

ASSIMILATION AND RESPIRATION MEASUREMENTS, PEKING SOY BEANS

Plant	Age in days	Mean temperature	Dry weight (gm.)	Leaf area (sq. cm.)	*Respiration:* gm. of CO_2 per 100 gm. (11 hours)	*Assimilation:* gm. of CO_2 per sq. m. of leaf area (13 hours)
A*	31	48	.....	.....	0.407	.....
	32	47.5	.....	.....	0.462	.....
	33	55.5	12.5	.....	0.541	.....
B*	31	91.4	.....	.....	0.890	.....
	32	94.0	.....	.....	0.850	.....
	34	90	10.5	.....	1.112	.....
C	18	47.5	.....	.....	1.28	.....
	19	47.5	0.78	.....	1.28	.....
D	18	90.5	0.73	.....	2.48	.....
E (2 plants)	9	63	0.315	.....	2.17	.....
F†	12	53.3	0.165	.....	2.19	.....
	13	82.8	.....	18.42	.....	29.32
G†	12	85.1	0.175	.....	3.17	.....
	13	84.3	.....	28.32	.....	27.89

* Plants A and B were cut and dried six days after the last respiration measurements were made.

† Assimilation measurements for plants F and G were made on the same day. Their dry weights were nearly the same, they had the same number of leaves, but on measurement it was found that the leaf area of the one was much greater than the other.

To control the temperature inside the bell jars during the middle hours of the day it was found necessary to erect a cheesecloth shade above the plants. The temperature as read from a thermometer with a protected bulb was not allowed to go above 90°.

The results given in table II indicate that respiration proceeded almost twice as rapidly in the hot night chamber as it did in the cold night chamber, and that a ratio of about fifteen to one existed between assimilation and respiration. Assimilation measurements were made on some of the larger plants, but due to their size, the

air passing through the bell jar was so depleted of carbon dioxide (to the extent of 50 per cent) that the results obtained were probably too low. In the cases given the CO_2 content of the air leaving the bell jar was 70–80 per cent of normal during the middle hours of the day. From the last two plants, F and G, it appears that assimilation was little affected by the temperature of the previous night, although the respiration of the hot night plant was almost double that of the plant in the cold chamber.

PHYSIOLOGICAL NIGHT.—In this experiment a second method of disturbing the assimilation respiration balance was tried. The plants were deprived of carbon dioxide for a number of hours each day. It was not possible to conduct this experiment until late in the season, by which time outside temperatures were too low for soy beans and the length of day too short for normal vegetative development. For these reasons the plants were grown in the greenhouse and electric lights used to supplement the normal length of day.

Four groups of Peking soy beans were planted in a tray October 4. They germinated October 13, and after the second day were given thirteen and one-half hours of light by supplementing sunlight in the late afternoon and evening with a 300 watt incandescent lamp, with a shade, suspended two and a half feet above the plants at germination. On and after the ninth day from germination, one group of these plants was given a seven-hour day by covering them with a light-proof earthenware jar between the hours of 3 P.M. and 8 A.M. A second group was inclosed in a glass bell jar above the plate already described, and supplied only with air from which the carbon dioxide had been removed. This treatment was continued during the same hours for which the first group of plants was covered with the light-proof jar. The bell jar was removed during the day. A third group was untreated, and a fourth group covered with a bell jar held above the soil, leaving a space of several inches at the bottom to admit air freely, but at the same time to simulate to some extent the temperature and light conditions which the plants under the other bell jar were receiving. The plants given the short days produced flowers on November 28. None of the plants in the other groups had flowered by December 24, at which time the

treatment was discontinued. The growths of the plants given the long dark night and of those given the "physiological night" were very similar, the plants attaining average heights of 10 and 13 cm. respectively. The other plants made a much greater growth than did the first two groups, the heights being 33 and 37 cm., the group partially inclosed within the second bell jar being again the taller.

If the premise of this second experiment is correct, it is possible, and perhaps probable, that the results obtained in the first experiment were purely the effects of nightly temperatures. If so, nightly temperature in its action upon plants does not produce the same response with all species, even though these species may react alike to shortened days. For this reason there are appended the following notes on the behavior of other plants, which were also given the higher and lower nightly temperatures. While the preceding has to do with nightly temperatures, there may be no special reason for believing that increased or decreased temperatures at another time than during the night might not also bring about differences in the growth and development of plants.

Effect of high and low nightly temperatures upon other plants

COTTON (Durango).—Under the cold night treatment the plants developed only a few tiny aborted leaves above the cotyledons, and then died. The cotton in the hot chamber flowered on August 7 (planted June 13). The plants bore heavily, and the growth was of a fruiting type. The check night plants made about the same growth, but it was of a more vegetative type; only a few bolls were set, these coming from flowers which opened in September, four days after the treatment had been stopped (fig. 2).

COSMOS (Lady Lenox and Klondike).—These plants flowered when given the thirteen-hour days in both the check and hot chambers. The plants in the check chamber were somewhat earlier than were those given the hot night, and the growth was more normal, and more dry matter was produced. Klondike cosmos in the cold night chamber made only a very feeble growth, and did not show signs of flowering until after the treatment was stopped. These varieties of cosmos are short day plants (fig. 3).

FIG. 2.—Durango cotton, showing effect of high night temperature (left with bolls) compared with check at right (leaves removed).

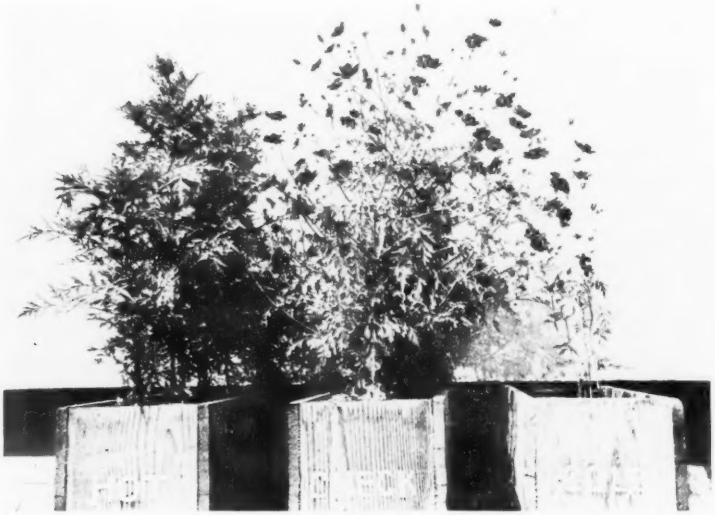


FIG. 3.—Klondike cosmos, showing relation of temperature treatment to blooming and growth.

PHLOX (perennial).—Well started roots, treated after May 9, flowered in the hot chamber July 7, in the cold chamber July 28, and in the check chamber August 7. There was only one plant of each.

ASTER (Crego).—Young plants were transplanted and treated after May 9. The plant in the hot chamber flowered August 10, in the check chamber August 29, and in the cold chamber September 1. Plants in the field flowered August 13.

RED CLOVER.—These were planted in the early spring and treated after May 9. They did not flower in either the cold or check chamber. Two plants out of eight grown in the hot night chamber flowered July 22. Field-grown plants flowered July 22.

LEMON TREES (Lisbon variety, on Sour Orange stock).—These young shoots from fall buds made in the cold chamber 37 cm. growth, check chamber 69 cm., hot chamber 46 cm., in the field with a normal day 76 cm., and with a 10-hour day 39 cm.

POTATOES (McCormick).—These were not started under the treatments until they were almost ready to flower. The plants in the hot chamber were less coarse, more upright, and made a greater top growth than did the plants in the cold or check chambers. These latter plants matured earlier than did the hot night plants. In yield there was very little difference, but when harvested the tops of the hot night plants had not started to die.

ZEA MAYS (Navajo).—Fig. 4 shows the hourly elongation of maize under different nightly temperatures. These elongation curves have no direct bearing upon the assimilation-respiration balance theme, but they are of some interest from the standpoint of the effect of nightly temperatures. The plants from which these elongation measurements were made were grown in the greenhouse in the fall of the year. The "hot" and "cold" nightly temperatures were about the same as for the summer experiments, but the temperature of the uncontrolled check was considerably lower.

Summary

1. The time of flowering of Peking soy beans given high, low, and uncontrolled nightly temperatures was affected to an extent comparable with the differences brought about by varying the length of day.

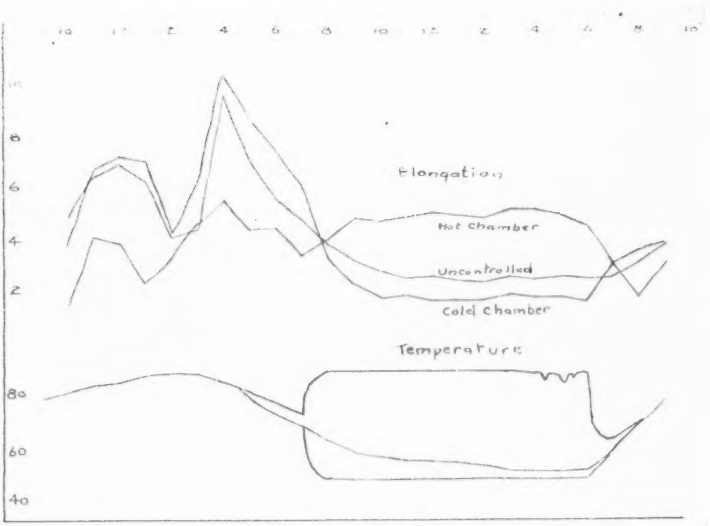


FIG. 4.—Elongation of maize given hot, cold, and uncontrolled temperatures during night; elongation in mm. per hour shows close relationship to nightly temperature.

TABLE III

MAIZE

	Cold	Check	Hot	Field
	Navajo, planted April 25, up May 3; treatment May 9–July 20			
Days "up" to pollen	64.4±0.45	54.6±0.31	55.4±0.41	.....
Days pollen to silk	1.6±0.56	0.0±0.36	7.0±0.56	.....
Total number of leaves	14.0±0.0	12.2±0.12	15.4±0.24	.....
Length of longest leaf	73.0±1.09	72.8±0.99	76.2±0.72	.....
Width of longest leaf	6.4±0.21	7.2±0.13	7.1±0.15	.....
	Northwestern Dent, planted July 10, up July 17; treatment started July 20			
Days "up" to pollen	45.8±0.36	38.6±0.49	39.0±0.47	40.3±0.46
Total number of leaves	12.8±0.18	12.4±0.31	16.2±0.40	14.3±0.16

2. It was found by measurements that respiration proceeded almost twice as rapidly under hot night conditions as under cold night conditions.

3. Depriving soy beans of carbon dioxide for a number of the hours of the day did not affect the time of flowering.

4. Not all short day plants gave the same reactions to varied nightly temperatures.

5. The elongation of maize during the night was found to be nearly proportional to the temperature.

The writer wishes to express his thanks to Mr. G. N. COLLINS, for his helpful suggestions during the course of these experiments, and to Dr. R. B. HARVEY, for his suggestions on the preparation of the data for publication.

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EFFECT OF ETHYLENE UPON RESPIRATION OF LEMONS[1]

F. E. DENNY

(WITH TWO FIGURES)

When lemons are received at the packing house, some of them, particularly in certain seasons, are green in color. Such fruit is regarded as commercially mature, and, in fact, represents a high market grade when the yellow color has been brought out by subsequent treatment. If these green lemons are sorted out, placed in boxes, and stored under suitable conditions, such as are obtained in basement storerooms, a yellow color develops in from one to two months. Practical experience has shown that the desired color can be obtained in from one to two weeks by placing the fruit in rooms heated with kerosene stoves. The experiments of SIEVERS and TRUE (**6**) showed conclusively that the coloration of the fruit in this forced curing method was brought about, not primarily by the conditions of temperature and humidity existing in the room, but by the gaseous combustion products generated by the kerosene stoves. As a result of this discovery, the common method employed at present consists in placing the kerosene burners in a separate building, called the generator room, and conveying the gaseous products to the various sweat rooms by conduits and electric fans.

Experiments were started by the Laboratory of Fruit and Vegetable Chemistry, Bureau of Chemistry, United States Department of Agriculture, to determine, if possible, the gaseous constituent of the sweat room atmosphere that was responsible for coloration of the fruit. Details regarding these experiments will not be described in this paper, but are to be published in a succeeding article. It is sufficient to state that ethylene was very effective in bringing about the desired result, concentrations as low as one part (by volume) of ethylene in one million parts of air being sufficient to cause green lemons to turn yellow in about six to ten days.

[1] Published by permission of the Secretary of Agriculture.

The experiments also showed that high concentrations of ethylene (80 per cent), high temperatures (92° F.), low temperatures (45° F.), and lack of oxygen either entirely prevented or greatly delayed coloring. Conditions suitable for the life processes of the fruit were favorable for coloring. Furthermore, coloring with either ethylene or gas from the kerosene stoves caused the loss of the "buttons" (calyx, receptacle, and a portion of the peduncle). A microscopical examination of the cells at the absciss layer showed that they had become enlarged and gelatinous. Apparently secondary growth had started in this area at least, producing a condition in lemons analogous to the extrusion of tissue on stems of various plants mentioned by Miss DOUBT (1).

These facts indicated that ethylene in some manner stimulated the growth, or the life processes of the cells of the fruit. If this were the case, the respiration of the fruit should be increased. The results of the measurements of the carbon dioxide output of ethylene treated lemons as compared with those receiving no ethylene are here recorded.

Methods

Fresh green lemons from a commercial packing house were selected for soundness and uniformity. They were sorted into lots of six or seven lemons and placed in glass desiccators (6–7 inches in diameter) provided with inlet and outlet tubes, arranged to draw a current of air through the system. Rubber stoppers were firmly tied and all rubber connections were covered with paraffin. The desiccators containing the fruit were kept in an incubator at 25° C. continuously, except for the periods during which air was being aspirated through them for the absorption of the carbon dioxide. At such times it was necessary to expose them to the laboratory temperature, which varied on different days from 18° C. to 22° C.

Once each day the fruit was thoroughly aerated, in one experiment by removing the desiccator covers for one-half hour and exposing the fruit to the outdoor air, and in another experiment by removing the fruit from the container, filling the container with water, emptying it, and replacing the fruit. Starting from the time of complete aeration, the carbon dioxide was allowed to accumulate, in the first experiment for 2.5 hours, and in the other for 1.5 hours.

The carbon dioxide was absorbed by a solution of barium hydroxide placed in Pettenkofer tubes, as recommended by GRAFE (2). Bubbles were aspirated through at the rate of about 2 liters per hour, in the first experiment for 2.5 hours, and in the other for 1.5 hours. The reduced pressure was regulated to about 1.3 cm. of mercury below atmospheric by a Palladin pressure regulator (GRAFE 2). Carbon dioxide was removed from the incoming air by soda lime tubes, and the outgoing air was tested for complete absorption by a bubbler of barium hydroxide.

At the end of the absorption period, the barium solution was washed into volumetric flasks with carbon dioxide-free water, made up to volume, and after the carbonate had settled to the bottom an aliquot of the supernatant solution was removed. The residual barium hydroxide was titrated with sulphuric acid standardized to a strength such that 1 cc. was equivalent to 1 mg. of carbon dioxide (OLSEN 5), using phenolphthalein as indicator. Each day a blank experiment with a desiccator containing no fruit, but to which was added one part ethylene to one thousand parts of air, was run. Titration values obtained with fruit were deducted from the titration values of this blank. Results were calculated to milligrams of carbon dioxide per kilogram of fruit-per-hour basis. Time was counted from the sealing of the desiccator to the end of the absorption period.

Effect of ethylene upon respiration

Lemons were divided into four lots. In two of the desiccators ethylene was added from a gas burette in quantities sufficient to make the concentration of ethylene within the desiccator approximately one part in one thousand, account being taken of the volume occupied by the fruit. The subsequent treatment of the different lots is shown in table I, the data of which are shown graphically in fig. 1.

At the end of the first day, the respiration of the ethylene treated lots was decidedly increased, although both lots did not respond equally well to the treatment. Lot 849 was given ethylene at a concentration of 1 part in 1000 at the end of the second day, and two days later the respiration had increased about 175 per cent.

After the respiration of lot 821 had been increased by the use of ethylene, a discontinuance of the ethylene applications led to a decrease. The rate of decrease after discontinuing ethylene was not so rapid as the rate of increase brought about by the original

TABLE I

EFFECT OF ETHYLENE (1:1000) UPON RESPIRATION OF LEMONS

LOT NO.*	TREATMENT	CARBON DIOXIDE (MG.) RESPIRED†					
		Start	First day	Second day	Fourth day	Sixth day	Ninth day
821.....	Ethylene added at start, discontinuing at end of second day	8.0	21.5	29.7	23.0	20.5	.....
832.....	Ethylene added at start, continued throughout	8.2	15.9	21.2	31.6	31.0	30.0
849.....	Ethylene added end of second day	6.8	8.2	9.7	26.7	29.7	.....
841.....	Check; no ethylene	7.7	12.0	8.7	9.0	8.0	12.9

* These numbers also represent the weight in grams of the sample used.

† Milligrams per hour per kilogram of fruit.

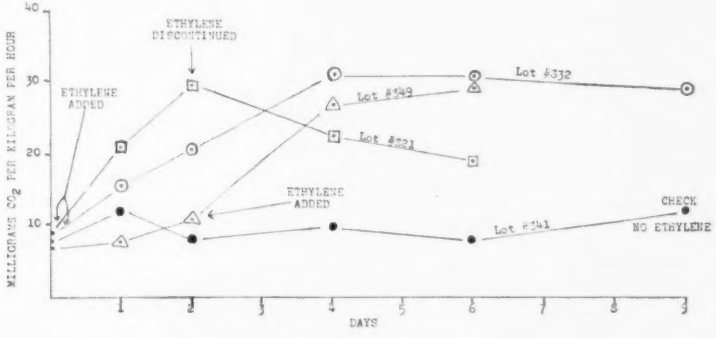

FIG. 1

application. The percentage increase due to ethylene cannot be calculated accurately from the data given, but it is apparent that the increase due to ethylene is of the order of 200 per cent. Lot 849 showed an increase of about 260 per cent.

The lot treated with ethylene throughout the experiment (no. 832) began to show yellowing about the third day. At this

time also the "buttons," because of growth of the cells below, were raised slightly and could be pushed off by pressure with the thumb. Full yellow color had developed by about the seventh day. The untreated fruit remained green and the buttons were firmly attached. These results are in accordance with numerous previous experiments on the effect of ethylene on the coloration of green lemons.

Effect of different concentrations of ethylene

In this experiment concentrations of one part in one thousand, one part in ten thousand, one part in one hundred thousand, and one part in one million were used. To obtain such concentrations, a Florence flask with a capacity of 1.5 liters containing outdoor air was provided with a rubber stopper and glass tube inlet. A few cubic centimeters of mercury was added to form a seal when the bottle was inverted. Into this bottle enough ethylene was pushed over from a gas burette to make a concentration of 10 per cent ethylene. From this as a starting point, concentrations of 1, 0.1, and 0.01 per cent ethylene were made by dilution, using similar flasks as containers. Ethylene from such flasks was added to the desiccators containing the fruit to make the desired concentrations in the atmosphere surrounding the fruit. The data are tabulated in table II and are shown graphically in fig. 2.

The fruit used in this experiment had a higher respiration rate and showed greater variability than that used for the first experiment. In the case of each concentration tried, however, application of ethylene resulted in an increase in respiration (fig. 2). The increases ranged from about 100 to about 240 per cent. Many more data are needed to permit an accurate statement of the percentage increase. There are indications that some samples of fruit are more sensitive than others to ethylene and give greater responses. While with the lot of fruit used in this experiment considerable variations on different days were found with untreated fruit, the coincidence in point of time between the application of ethylene and the rise in respiration is proof that the rise is due to the ethylene.

While all the concentrations used caused an increase in respiration, 1:1,000,000 was less effective than stronger concentrations,

TABLE II

EFFECT OF DIFFERENT CONCENTRATIONS OF ETHYLENE UPON RESPIRATION OF LEMONS

Lot no.*	Treatment	Carbon dioxide (mg.) respired†					
		First day	Second day	Third day	Fourth day	Sixth day	Eighth day
736.....	Ethylene 1:1000 added at end of third day, continued throughout	13.8	.....	9.7	26.1	31.7	41.0
728.....	Ethylene 1:1,000,000 added end of fourth day, continued throughout	15.9	.....	16.9	13.1	25.0	31.6
729.....	Ethylene 1:100,000 added end of third day, discontinued end of sixth day	20.1	.....	16.5	17.4	42.8	28.9
716.....	Ethylene 1:10,000 added end of sixth day	20.1	.....	20.5	11.4	17.2	54.0
763.....	Check; no ethylene	.....	15.4	17.4	12.7	17.0	18.6

* These numbers also represent the weight in grams of the sample used.
† Milligrams per hour per kilogram of fruit.

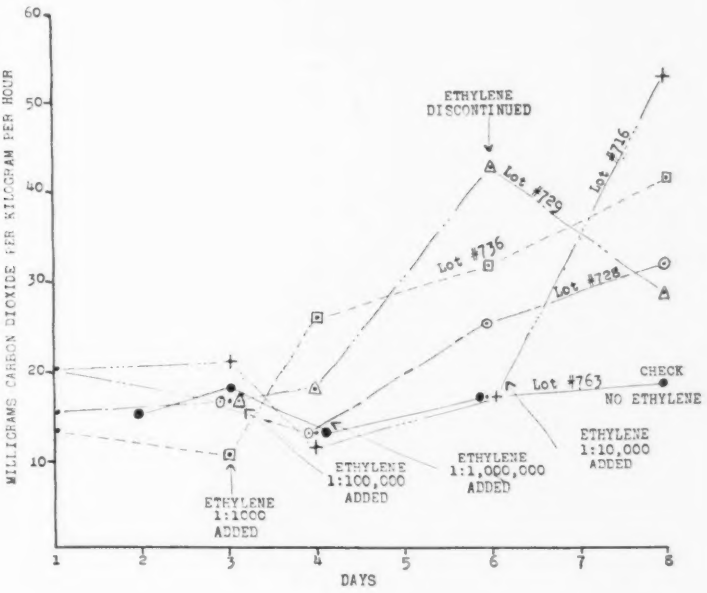

FIG. 2

indicating that the limit of dilution was being approached. There are also indications (fig. 2) that 1:1000 was too strong for best results, and that concentrations of 1:10,000 and 1:100,000 had a greater stimulating action. A larger number of experiments would be necessary to decide this point conclusively, however.

Discussion

No previous work appears to have been done on the effect of ethylene on the respiration of lemons; in fact, only one reference relating to the effect of ethylene upon the respiration of any plant was found. HARVEY (3), working with sweet pea seedlings at ethylene concentrations of 0.0002 per cent (by volume), found a depression in carbon dioxide output in every case but one. An essential difference in these two experiments should be noted. The sweet pea seedlings were undoubtedly in a state of active growth, while the lemons had practically completed their growth and were in a relatively dormant condition; hence the factor of toxicity should operate more strongly upon the sweet pea seedlings than upon the lemons. Thus a difference in the behavior of the two might be expected.

The exceptional case found by HARVEY is interesting in this connection. With the shortest period of exposure to ethylene, the 3-hour period, he found that the ethylene treated lot showed an increased respiration over the check lot. A stimulative action producing an increase in carbon dioxide production shortly after the application of the gas, before the anaesthetic effects could become apparent, would be in agreement with the results obtained by IRVING (4). Investigating the effect of chloroform vapor upon the respiration of barley and cherry laurel leaves, IRVING found that the response depended upon the concentration used. Low concentrations gave increases that were maintained during the entire experimental period. High concentrations depressed the respiration in every case. Medium concentrations caused an "initial outburst" of carbon dioxide, an expression that was justified by the data. Thus in one case he found that the respiration was increased 200 per cent (trebling the rate) after one hour's exposure. The percentage increase in this case is of the same order as that found in the experiments with lemons here reported.

IRVING's data show that the high initial rates with these medium concentrations were not maintained, but were later followed by a decrease. With lemons, however, the rate produced with the strongest concentration (1:1000) was maintained fairly well for five days, with only a slight decrease (lot 832, fig. 1); hence there is evidence of only low toxicity, if the toxicity may be judged by fall in rate of respiration. The concentrations used appear to be stimulative rather than depressive.

Summary

1. Ethylene at concentrations of one part in one thousand of air, one part in ten thousand, one part in one hundred thousand, and one part in one million increased the respiration of green lemons. The effect appeared to be greatest at the intermediate concentrations, although more work to establish the concentration yielding the maximum effect is necessary.

2. The increase in carbon dioxide output ranged from about 100 per cent to about 250 per cent.

3. After the respiration of a given lot of lemons had been increased by the use of ethylene, a discontinuance of the ethylene applications led to a decrease.

4. Yellowing of the ethylene treated fruit became visible about the third or fourth day, and full yellow color was developed in six to ten days. Untreated fruit remained green during the same period of time.

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GROWTH OF PLANTS IN ARTIFICIAL LIGHT

II. INTENSITIES OF CONTINUOUS LIGHT REQUIRED FOR BLOOMING

ESTEN HENDRICKS AND R. B. HARVEY

(WITH ONE FIGURE)

The intensity of light at which plants are grown is related to the rate of growth. In continuous illumination there is a constant rate of synthesis of carbohydrates, and the rate of growth is uniform. Under such conditions there is no periodic daily fluctuation in carbohydrate content or in growth rate, such as occurs in plants which are grown in sunlight. By the use of Mazda lamps as the source, the intensity of light can be kept fairly constant, so that one can determine definitely what intensity is required for maintenance of the plant or for flower production. KRAUS and KRAYBILL[1] have shown that fruiting is dependent upon a certain ratio of carbohydrates to other nutrient constituents; so one would expect blooming to be dependent upon a suitable intensity of light.

From common experience it is observed that plants vary in their requirements of light intensity. It was the object of this study to determine what these requirements are, when temperature is kept constant and other environmental factors are held as nearly uniform as possible. Obviously, the light intensity required for the continued growth of a plant must be such that the assimilation will at least overbalance the loss by respiration.

Plants were grown in the rooms described in a previous paper.[2] They were planted in good soil and watered with Knop's nutrient solution occasionally, so that there was no deficiency of mineral nutrients. The light intensity was varied by placing the plants at different distances from the lamps. The Macbeth illuminometer was used to measure light intensity, reading directly in foot candles.

[1] KRAUS, E. J., and KRAYBILL, H. R., Vegetation and reproduction with special reference to the tomato. Oregon Agric. Coll. Exp. Sta. Bull. 149. 1918.

[2] HARVEY, R. B., Growth of plants in artificial light. BOT. GAZ. 74:447–451. 1922.

Where there was a considerable increase in height of the plants as they grew, the intensities are given over the range covered. Several measurements of light intensity were taken during the period of growth. The plants were subjected to a range of intensity from 50 to 10,632 foot candles. Only the intensities at which the plants bloomed are recorded in table I. No doubt in the higher intensities some varieties were subjected to excessive temperatures, owing to the light absorption by the leaves. Since in most cases the plants were grown from seed, they assimilated practically all of their dry weight in the artificial light.

Amaranthus retroflexus and *Chenopodium album* bloomed at notably high light intensities, but were stockier than those plants which bloomed at lower intensity. Evidently these plants have a high tolerance for light. Strawberries bore fruit at 1500–2000 foot candles, but did not bloom at 500 foot candles. Plants grown at intensities below their proper range tend to be spindling, and are likely to become diseased. *Nicotiana tabacum* grew well at low intensity and bloomed over a great range of intensity. *Fagopyrum* and *Tropaeolum* seem adapted to growth at low intensities, in fact at intensities at which a great many plants cannot maintain themselves.

The four-o-clock produced abundant flowers at 1350 foot candles, but only by violent fluctuations in temperature or moisture could the flowers be opened in continuous light. When the temperature and soil moisture were kept uniform, the flowers remained unopened although fully formed, until an abscission layer formed and they dropped off. After a number of flowers were fully formed and past the time at which they should have opened, the lights were turned off for an hour. Then ten flowers promptly opened. Squash produced staminate flowers abundantly at 476 foot candles, but only a few pistillate flowers.

On December 27 some Easter lily bulbs were just sprouting. The plants shown in fig. 1 were photographed on February 27. The lily on the left was grown in continuous artificial light at 20° C., the one on the right was grown in the greenhouse at a fluctuating temperature which averaged above 20° C. In artificial light Easter lilies can be speeded up to bloom within two months after sprouting. The plants in the greenhouse did not bloom until a month later.

TABLE I

INTENSITIES OF LIGHT AT WHICH PLANTS BLOOMED AND PRODUCED SEED

Plant	Temperature °C.	Light intensity in foot candles
Boltonia asteroides	25	950
Cucurbita moschata*	25	550
Pisum sativum	14	400
Silene latifola	25	800
Lactuca sativa	25	900–1350
Erigeron canadensis	25	1040
Melilotus alba	14	1180
Phaseolus vulgaris	25	850
Stellaria media	25	920
Avena sativa	14	950
Hordeum vulgare	14	650–800
Secale cereale	14	600–1200
Triticum vulgare (Kota)	14	650–800
Triticum vulgare (Winter)	14	650–800
Triticum vulgare (Bluestem)	14	650–800
Triticum durum (Monad)	14	650–800
Raphanus sativus	14	1400
Trifolium pratense	14	1400
Melilotus officinalis	14	1400
Viola tricolor*	25	1000
Tropaeolum minus	20	250–450
Oxybaphus nyctagineus	20	1350
Cucurbita moschata	20	250–500
Linum usitatissimum	20	500–1050
Nicotiana tabacum	20–25	800–10,032
Zea Mays	25	500–3000
Euphorbia splendens	20	800
Lilium longifolium	20	1200
Salvia sp	20	300
Pelargonium sp	20	350–550
Trifolium hybridum	20	400–600
Chenopodium album	20	500–10,632
Amaranthus retroflexus	20	500–10,632
Solanum nigrum	20	750
Phaseolus vulgaris	20	300–550
Cannabis sativa	20	300–450
Dianthus barbatus	20	650
Fragaria sp	20	1500–2007
Cucumis melo	20	500–2007
Fagopyrum esculentum	20	300–400
Hibiscus trionum	25	600–900
Solanum tuberosum*	25	450–500
Curcurbita Pepo*	25	500–750
Aster sp	25	500–2007
Viola sp	25	.....

* Bloomed but no seed set.

Evidently the quantity of material assimilated by the leaves serves to increase the growth rate over that of plants with day and night

FIG. 1.—Plant on right grown in daylight; plant on left grown in continuous artificial light.

TABLE II

CARBOHYDRATES OF EASTER LILY*

SAMPLE†	DRY WEIGHT PERCENTAGE	SUGARS			STARCH PERCENTAGE	PENTOSAN PERCENTAGE	TOTAL NITROGEN PERCENTAGE
		Reducing percentage	Sucrose percentage	Total percentage			
Daylight.....	10.91	3.23	6.22	9.45	2.35	6.96	3.34
Artificial light....	9.78	10.51	2.92	13.43	6.41	8.89	2.34

* The writers are indebted to Mr. F. R. DAVISON for these analyses.

† Both samples picked at 3:00 P.M., March 20, 1923; samples run in duplicate or triplicate.

exposure. In table II is given the composition of the lily leaves collected at 3:00 P.M., when the plants in daylight should show a maximum of starch. The greater quantity of carbohydrates in the plants grown in artificial light is quite marked.

Conclusions

1. A number of plants have been subjected to continuous artificial illumination and determinations made of the light intensities at which blooming occurred.

2. Plants were found which showed growth and blooming at a great range of intensities, while others were found to bloom only at a limited range.

3. A speeding up of the time of blooming in Easter lilies was correlated with an increase in the carbohydrate content of the leaves when grown in continuous artificial light.

UNIVERSITY FARM
ST. PAUL, MINN.

SMOKE AND SOIL ACIDITY

ARTHUR PIERSON KELLEY

(WITH TWO FIGURES)

The southern part of the "peninsula" upon which the city of Philadelphia is built is a slightly undulating plain with an elevation varying from sea level to thirty feet. For many years civic growth was in other directions, while this southern area remained as a region of small truck farms, but houses and factories are now encroaching upon it. With this industrial development have come repeated complaints from the truck farmers that their crops were damaged by various emanations from the nearby factory stacks. At the suggestion of Professor RODNEY H. TRUE, to whom the writer is much indebted for advice during the prosecution of the work, a soil survey of the region was undertaken to determine whether or not the agricultural soils of the region were acid, and if acidity were present, whether its distribution could be correlated with fume production from the industrial plants. If these plants were giving off considerable quantities of acid fumes, it seemed probable that these would have accumulated in the soils of the region in such quantities as could be measured by the methods here used.

Investigation

SOIL.—The area investigated, including about three square miles, is part of the coastal plain, and is covered by an alluvial deposit called Sassafras soil,[1] formed from weathering of unconsolidated deposits of late geological age. Sassafras sandy loam consists of a light brown or yellowish gritty sandy loam becoming heavier with depth. Both soil and subsoil contain mica flakes and fine gravel. In places the latter is found in considerable quantities. Almost surrounded by towns, with rivers on three sides used by many steamers, the land intersected by railroads and dotted with factories, it would seem that the region might be subject to smoke injury.

[1] SHAW, C. F., Soils of Pennsylvania. Penn. Agric. Exp. Sta. Bull. 132. 1914.

ACIDITY OBSERVED.—Work was done in this region during the months of July and August, 1922, on both cultivated and uncultivated land in different parts of "The Neck" at varying distances from the most conspicuous plants. Borings were made with a soil auger to levels from 15 to 90 cm., and the samples thus obtained were carried immediately to the laboratory in corked test-tubes. Here they were mixed with distilled water in 1:3 proportion and

TABLE I

P_H VALUES

TEST BORINGS NO.	DEPTH OF SAMPLES IN CM.						
	Surface	15	30	45	60	75	90
2261	5.6	6.0	6.0	5.8	5.8	6.1	6.1
2268	6.0	5.7	6.1	6.1	6.4	6.5	6.5
2275	6.2	5.7	5.6	5.8	5.8	5.9	6.0
2282	6.2	6.0	6.1	6.2	6.2	6.4	.....
2288	6.2	5.6	5.4	5.7	5.7	5.7	.....
2221	5.6	5.6	5.8	5.8	.....	.....	.....
2228	5.8	5.6	5.6	.....	.....	.....	.....
2000	5.0	5.1	5.3	5.5	5.8	5.8	6.0
2007	5.5	5.6	5.6	5.6	5.6	5.8	6.0
2014	5.6	.....	.....	.....	.....	.....	.....
2021	5.6	5.6	5.7	5.6	.....	.....	.....
2028	5.6	5.6	5.6	.....	.....	.....	.....
2035	5.8	5.6	5.1	4.9	5.7	5.8	5.8
2042	6.1	5.6	5.4	5.6	6.0	6.1	6.3
2091	5.4	5.8	6.4	6.8	6.8	6.8	6.6
2305	6.0	5.7	5.4	5.6	5.8	5.4	5.4
2312	5.8	6.0	6.8	6.8	7.0	7.0	7.0
2319	6.0	5.6	5.6	5.8	5.8	6.1	5.9
2326	6.0	6.1	6.1	6.3	6.1	6.4	6.7
2333	6.0	6.0	5.6	5.8	5.8	5.4	.....
2340	5.4	5.4	5.6	.....	5.8	5.9	5.9
2347	5.4	5.6	6.0	6.0	.....	5.4	5.8
2354	5.6	5.8	5.8	6.0	6.0	6.0	6.0
Average	5.75	5.69	5.75	5.84	6.35	6.47	6.13

tested with Clark and Lubs indicators by the use of a comparator and standards. The results of these tests are shown in table I. It will be seen that the soils are acid, but that the geographical evidence seems to indicate that the acidity is not to be correlated with any one industrial plant (fig. 1). Being almost encircled with smoke sources, the atmosphere of "The Neck" would be smoky no matter what the direction of the wind. Moreover, soil

immediately adjoining the most important works was not acid. Similar results have been found by JUST and HEINE.[2]

SMOKE AND ACIDITY.—A question now arose as to whether acidity found in the soil was caused by smoke, or whether it was a natural condition of Sassafras soil. To determine this an investigation has been made of a comparable area of Sassafras loam at Monmouth Junction, New Jersey, where the atmosphere, while not entirely free from smoke, was much more nearly so than in South

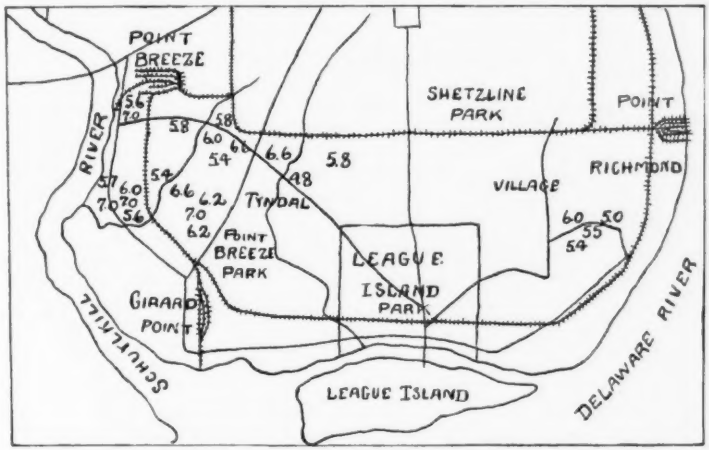

FIG. 1.—Map of South Philadelphia; figures indicate P_H values

Philadelphia. The results are given in table II. In general a sandy soil may be normally acid, as indicated by a DeKalb area in the North Valley Hills of Chester County, Pennsylvania. A more or less similar curve on the acid side is again exhibited (fig. 2).

SOIL ACIDITY AND SULPHUR.—Tests were made to discover the sulphur dioxide content of soils from various places near the Point Breeze works. They were carried out according to the method given by HAYWOOD,[3] and the results are given in table III, together with some obtained for soils from Monmouth Junction, New Jersey,

[2] JUST, L., and HEINE, H., Zur beurteilung von vegetationschaeden durch saure gase. Landw. Versuchs-Sta. **36**:135–158. 1889.

[3] HAYWOOD, J. K., Injury to vegetation by smelter fumes. U.S. Dept. Agric. Bur. Chem. Bull. 113. 1908.

and from Paoli, Pennsylvania. Waters flowing out of the region apparently are contaminated by sewage. Two natural streams remain, and there are a number of drainage canals, especially in

TABLE II

P_H VALUES

TEST BORINGS NO.	DEPTH OF SAMPLES IN CM.				
	Surface	15	30	45	60
1178	6.0	6.0	5.8	.....	.....
1183	6.2	5.7	5.6	5.6	.....
1187	5.7	5.7	5.3	5.3	5.3
1192	5.4	5.8	6.0	6.1	6.1
1202	4.4	4.5	4.6	5.2	5.0
1499	6.0	5.8	6.0	6.0	6.0
1504	5.8	5.9	6.0	6.6	6.6
1509	6.0	5.6	5.8	6.0	6.2
1514	6.4	6.1	6.2	6.4	6.4
1520	5.8	6.0	6.2	6.4	6.0
1525	6.3	6.5	6.8	7.0	6.4
1530	6.2	6.1	5.8	5.4	5.6
1535	6.0	5.8	6.0	6.4	6.4
1547	5.4	5.2	5.8	5.6	5.8
Average	5.82	5.75	5.83	6.00	5.98

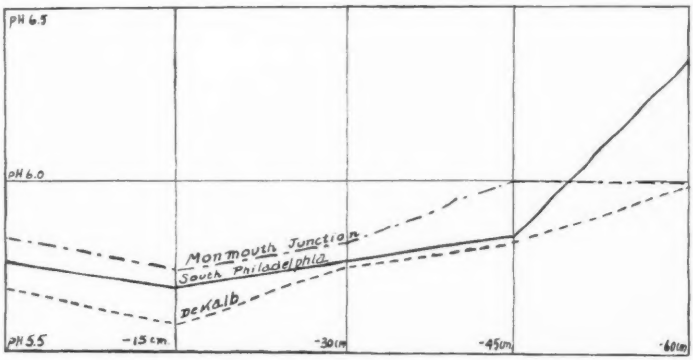

FIG. 2.—Relation of soil depth to soil acidity; figures indicate P_H values

the lower lying eastern section, the waters of which in all cases observed were over P_H 7.0. Dew on plants at Remerten's Nurseries at least on one day was about P_H 7.0, while at other times and in

other places the P_H was less, to as low as 5.6. Even in an area subject to smoke influence soil may not of necessity be acid, nor crops seriously affected. A half-acre garden on Manor loam at Paoli, Pennsylvania, almost constantly under an atmosphere laden with fumes blown over from the railroad yards, was kept under close observation. With constant cultivation during the growing season and proper use of fertilizers, the soil is kept at a P_H about 7.0, although Manor loam is normally at a P_H of 6.4.

TABLE III

Test borings no.	Location	Percentage SO_4, as $BaSO_4$	P_H
2	Grounds of Atlantic refinery	1.37	7.0
6	Overgrown field, Girard Point	1.33	5.6
7	Marsh, Girard Point	1.32	5.4
8	Hay field, Girard Point	1.38	6.6
20	Cultivated field, Girard Point	2.91	6.6
28	Garden, Monmouth Junction, N.J.	0.74	6.1
38	Field, 1 mile from railroad, Paoli	2.44	6.4
40	Garden, cultivated, Paoli	3.16	7.2
42	Garden, uncultivated, Paoli	2.23	6.8

Summary

In the trucking section of South Philadelphia the air is often heavily loaded with combustion products from great industrial plants, railroad engines, and other sources. The soils of this region, consisting of Sassafras loam, are somewhat acid but not more so than another area of the same soil type at Monmouth Junction, New Jersey, where there is little smoke. Other sandy soils, of DeKalb areas, have shown approximately the same P_H values. The geographical distribution of acidity in South Philadelphia apparently is not correlated with the location of the smoke producing plants. With better cultural methods, cultivated lands in another type of soil have been kept near neutrality.

UNIVERSITY OF PENNSYLVANIA
PHILADELPHIA, PA.

BRIEFER ARTICLES

THREE SETS OF MEGASPORANGIATE CONES PER YEAR IN PINUS[1]

(WITH TWO FIGURES)

Professor W. E. DAVIS called my attention during the spring of 1923 to a certain specimen of *Pinus Banksiana,* which he had been passing every few days, as exhibiting something very peculiar to him. Investigation showed that this tree was producing two and three sets of "yearly growths" during this spring, each of which had a bare space at the base where the microsporangiate cones normally occur. The leaves were as usual, and near the tip of each "year's growth" there were one or two (and in one case three) megasporangiate cones. At least four branches were found in which there were present three complete sets of megasporangiate cones, one set for each "year's growth." Several were found in which they were in the first and second or first and third "year's growths." When observed in the middle of the growing period, the different growths were progressively smaller in diameter, and had progressively smaller leaves, but the megasporangiate cones were practically all of the same size. Several small side branches produced the microsporangiate cones. In all such cases only the normal year's growth took place.

The tree was medium sized, a little under three meters in height, and had been transplanted to this spot at least four years previously. The growth was very vigorous on the branches as well as on the leaders. The peculiar growth took place in 1922 also, but more sparingly. Previous to that it apparently had not taken place.

Inspection of the cut ends showed the proper number of annual rings of normal size in accordance with the actual age, but closer examination with a compound microscope disclosed the fact that in at least some of the cases there were faint rings within the conspicuous annual rings, the same in number as that of the apparent "year's growths." During the period of growth in length one could tell the "year's growths," both by the thickness and by the fact that the newest growth was green throughout, but in the older "year's growths" of this year one or two layers of whitish

[1] Contribution from the Botanical Laboratory of Kansas State Agricultural College, no. 205.

FIG. 1.—End of branch of *Pinus Banksiana* Lamb, showing three sets of megasporangiate cones produced in 1923.

wood were evident. As the twigs increase in age the faint rings usually vanish. Consequently, later in the season or in later years the growths can be told apart positively only so long as they are of a size, or retain their cones, or have similar aged branches.

C. S. SARGENT, in his *Manual of the trees of North America*, in describing the cones, states for this pine: "Often with two clusters produced on the same shoot." This has been noticed previously on *Pinus Banksiana*

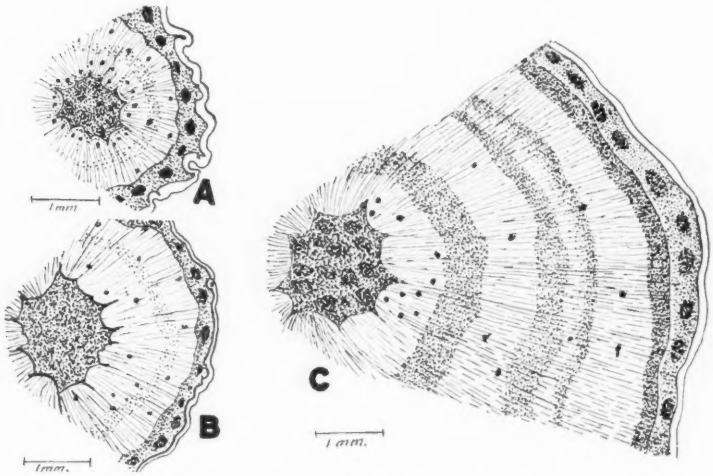

FIG. 2.—Diagrammatic sketches of cross-sections of twigs of *Pinus Banksiana* of different ages, collected in the fall: *A*, youngest or last of three growths produced in 1923; *B*, oldest or earliest of three growths produced in 1923; *C*, three-year-old twig, latest growth as shown by cones; sketches by S. FRED PRINCE.

in this vicinity, but at the present time this case is the best one that has been found, in which three sets of megasporangiate cones have been produced in a single year. At least five other trees of this species have been found which produced three growths in a year, although but sparingly. Both 1922 and 1923 have been prominent in this respect, although the seasons were quite different, that of 1922 being an early spring, while the spring of 1923 was very late. The summers were similar, although that of 1922 was very much hotter.—FRANK C. GATES, *Kansas State Agricultural College, Manhattan, Kansas.*

LACTOPHENOL

Investigators and teachers of natural science have need for a single solution in which freehand sections and small specimens of plants and animals can be fixed, stained, preserved, and permanently mounted. Lactophenol, a solution which partly accomplishes this purpose, was called to my attention by Dr. J. J. DAVIS of the University of Wisconsin. After using lactophenol for several years for various purposes, it seems desirable to call the attention of teachers and investigators to its merits.

A translation from STRASBURGER-KOERNICKE, *Botanisches Praktikum*, Fünfte Auflage, 767, 1913, follows:

Lactophenol: Lactophenol may be used alone or with copper solutions as a preservative material for mosses and algae. Lactophenol may be prepared:

1. Carbolic acid crystals	(c.p.)	20 gm.
2. Lactic acid	(sp. gr. 1.21)	20 gm.
3. Glycerine	(sp. gr. 1.25)	40 gm.
4. Water	(distilled)	20 gm.

This solution combines the clearing qualities of carbolic acid with the softening properties of lactic acid. It is very good for herbarium materials, especially when warmed with a 10 per cent lactophenol solution and transferred to pure lactophenol. For preserving desmids, Palmellae, and filamentous algae, place 5 gm. lactophenol with 95 cc. distilled water, then add 0.2 gm. copper acetate. This same solution, ten times more concentrated, is recommended for use on excursions. Place 5–10 per cent of the concentrated solution in water containing algae, which it fixes so that it can be stored for a long time. The chlorophyll holds its color in this solution. Glycerine gelatine may be employed as a mounting medium. Soak 8 gm. of gelatine in 44 cc. distilled water, then add 30 gm. glycerine, cook in a water bath, filter, and add 10 gm. lactophenol thereto. The preparations become as transparent as in Canada balsam, and are well preserved. Instead of lactophenol, one can add a concentrated lactophenol-copper solution to glycerine jelly. Green and blue pigment are well preserved.

Lactophenol gum as a mounting medium: dissolve 38 gm. very pure gum arabic in 50 cc. fresh distilled water, add 5 gm. glucose, 6 gm. lactophenol, and filter the solution through glass wool. It is used cold and dries very quickly.

In mixing the solutions composing lactophenol as described in this formula, the uncorked bottle of carbolic acid crystals should be set in a dish of water, and heat applied slowly until the crystals are in solution. The remainder of the process in preparing the formula needs no explanation.

An acid stain may be added to lactophenol when either differential staining or preservation of colors is desired. Stains used with best success by the writer are saüregrün, acid fuchsin, and acid carmine. A stock solution of green lactophenol was prepared by adding 0.10 gm. of Grubler's säuregrün to 100 cc. lactophenol. This stock solution may be used undiluted, or diluted by placing 10 cc. of green lactophenol into each of three pipette bottles containing 10 cc., 20 cc., and 40 cc. of clear lactophenol respectively. Experience showed different materials required different intensities of the colored stock solutions, and by this method three good working colored solutions were at hand. Generally, colored solutions of lactophenol were prepared by adding the stain to lactophenol until the solution gave a deep color when examined by transmitted light. Permanent sections should be mounted in a deep colored lactophenol solution, since the stain fades when exposed to bright light.

When microscopic slides containing sections mounted in lactophenol were stored, evaporation took place. If more lactophenol was flowed under the cover glass and the process repeated, evaporation was reduced to a minimum. If the slides and covers were cleaned and ringed with a good cement, however, evaporation of the lactophenol was entirely prevented and the mounted materials remained in an excellent state of preservation. While lactophenol has its limitations, when once used in the laboratory it will meet a long felt need.—W. H. DAVIS, *Massachusetts Agricultural College, Amherst, Mass.*

CURRENT LITERATURE

NOTES FOR STUDENTS

Photosynthesis and respiration.—In their studies of the physiological processes of green leaves, BROWN and ESCOMBE showed that leaves utilize in photosynthetic activity about 0.66 per cent of the radiant energy they receive. Furthermore, they calculated that if the leaf could utilize all the energy of that part of the spectrum in which chlorophyll absorbs most strongly, the efficiency of energy transformation would not exceed 6 per cent, since those regions of the spectrum contain only about 6 per cent of the total solar energy. WARBURG and NEGELEIN[1] have obtained a theoretical efficiency of energy transformation of 70 per cent, using a narrow region of the spectrum, 645–570 $\mu\mu$, and an intensity about 1/1000 of normal daylight. The light was thrown into cultures of *Chlorella* of such thickness as to give total absorption, and the energy transformation was calculated from the amount of O_2 liberated, corrections being made for respiratory use of oxygen. The observed efficiency was about 50 per cent, from which was calculated the initial efficiency for the first increment of light above zero. This extrapolated efficiency was 70 per cent.

Cells grown in weak light previous to use in experiments gave a higher efficiency than cells grown in strong light. This is explained on the basis of an adsorption theory which has been developed by WARBURG[2] with reference to photosynthesis and respiration. The photosynthetic reactions are considered to be adsorption reactions, and in brightly illuminated cells there is more free glucose. This glucose is adsorbed on the phase surfaces to a degree that retards the adsorption of the substances reacting in synthesis. As there are always some adsorbable substances present in the cells besides the reactive ones, and as the energy adsorbed by the chlorophyll is available for photosynthesis only during 10^{-8} seconds, it is evident that perfect efficiency is impossible. Evidence resulting from the application of the quantum theory to these problems lends support to such theories as have been put forward by WILLSTÄTTER and DIXON, who believe that the first reactions of photosynthesis involve intramolecular rearrangements either in H_2CO_3 or in the chlorophyll itself. In order to secure the requisite energy, one molecule of H_2CO_3 must interact with three molecules of chlorophyll.

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[1] WARBURG, O., and NEGELEIN, E., Über den Energieumsatz bei der Kohlensäureassimilation. Arch. Neerl. Physiol. de l'homme et des animaux. **7**:415–430. 1922.

[2] WARBURG, O., Über Oberflächenreaktionen in lebenden Zellen. Zeit. Elektrochem. **28**:70–75. 1922.

The importance of adsorption in respiration has been illustrated by means of a model cell, in the second paper cited. This consists of a solution of amino acids containing powdered charcoal. On passage of a current of air through the liquid, oxidation of the amino acids occurs at a rate equal to the respiration of an equal mass of living tissue. The charcoal, by adsorbing the interacting amino acids and oxygen on its surface, causes the reaction to be greatly hastened. Similarly, the great acceleration within the cell of processes that are infinitely slow outside it, WARBURG believes to be due to the adsorption of the reactive substances on the surfaces of the solid constituents of the cell.

The effects of anaesthetics upon living cells, and upon this model cell of powdered charcoal, are very similar. Thus, for the same degree of depression of respiration or photosynthesis, homologous series of anaesthetics show a progressive anaesthetic efficiency from member to member, the highest member of a series being from 100 to 1000 times as effective as the first member. On calculating the surface area covered by the anaesthetics at equal depression of the respiratory rate, it is found to be a constant. This constitutes strong evidence of the correctness of the theory. Moreover, these anaesthetics affect the oxidation of amino acids in the charcoal-containing model cell in exactly the same way as they affect the life processes.

The anomalous behavior of HCN which, although adsorbed quite weakly, is effective in suppressing respiration in very low concentrations, leads to the hypothesis that the surfaces of the solid cell constituents are mosaics of Fe-containing and Fe-free regions, the latter greatly predominating. Respiration and photosynthesis are supposed to be catalysed on the Fe-containing regions only, although the reacting respiratory and synthetic substances are adsorbed equally over the whole surface. The hydrocyanic acid, because of its strong affinity for the heavy metals, replaces the reactive substances only on the iron-containing areas, and thus little is needed to depress respiration, whereas anaesthetics replace them over the entire surface equally, and much is required unless adsorbed strongly. The rôle assigned to iron here is quite in accord with that put forward by MOORE some years ago. Such careful fundamental theoretical work as this is highly inspirational.—H. S. WOLFE.

Plant tumors and animal cancer.—LEVIN and LEVINE,[3] in a series of articles designed primarily for medical readers, endeavor to shed light upon certain aspects of the cancer problem through studies of similar growths in plants. They take exception to the view that cancer and crown gall are practically identical biologically, but consider that there are many points of analogy

[3] LEVIN, I., and LEVINE, M., Malignancy of the crown gall and its analogy to animal cancer. Jour. Cancer Research **5**:243–260. 1920.

———, The rôle of neoplasia in parasitic diseases of plants. Jour. Cancer Research **7**:171–178. 1922.

———, The action of buried tubes of radium emanation on neoplasias in plants. Jour. Cancer Research **7**:163–170. 1922.

between the two, and that since a plant is much less complex in its organization than an animal, neoplasias in plant tissues offer favorable material for studies of cell proliferation. It is claimed that crown gall in plants is commonly analogous to benign tumors in animals, and that malignant crown gall, while analogous to cancer, is relatively rare and is not due directly to infection by *Bacterium tumefaciens*, but rather represents the result of the action of an unknown secondary stimulus, which has altered the limited growth, begun for purposes of protection against bacterial invasion, into a condition of limitless proliferation.

It has long been noted that in club root caused by *Plasmodiphora brassicae* the large cells containing the parasite are always surrounded by layers of uninfected small cells. A similar condition occurs in potato wart lesions. The theory is advanced that these smaller cells are immune to the parasite and tend to form a protective barrier against its further encroachments.

The treatment of animal tumors by the insertion of capillary glass tubes filled with radium emanation demands a more complete knowledge of the mechanism of the radium action. For this investigation, also, plant tissues suggested themselves as favorable material. The effect of the radium emanation on both normal and diseased tissue was studied. The radium tubes were inserted as in animal tissues, and in every case empty glass tubes of similar size and shape were inserted into corresponding tissues as checks. Where normal tissue was used the radium emanation invariably induced necrosis, usually slight, but varying in degree according to the amount of radium emanation in the tube, the length of the exposure and the kind and age of the tissue. No necrosis was observed in the checks. Inoculation of *Pelargonium* stems with the crown gall organism, followed immediately by the insertion of the radium tubes, resulted in the formation of a black necrotic area around the tubes, but no galls were produced. Inoculated stems into which the empty tubes were inserted developed typical crown galls. If the introduction of the radium tube was delayed until the gall had developed, there was death of cells and necrosis in the region immediately adjacent to the tube, but cells beyond were morphologically unaffected. Earlier work is cited, however, suggesting that such cells have been so influenced by the gamma rays as to have had their proliferating power inhibited. Similar results were secured on club roots artificially produced in cabbage and kohlrabi by inoculation with *Plasmodiophora brassicae*.—G. W. MARTIN.

Shape of parenchyma cells.—If college students in botany were asked to describe the 3-dimensional shape of a typical plant cell, their replies would probably include the range of opinion that it is "six-sided" (cubical?) to irregularly polyhedral; a few might state that its shape is that which a plastic sphere would assume if surrounded by other similar spheres all of which touched; some might describe this "flattened sphere" as a rhombic dodecahedron. The latter is indeed the opinion that dates back to KIESER and BUFFON, who

arrived at this conception by the analogy of a stack of cannon balls, or of dry peas which are made to swell in a closed chamber. LEWIS,[4] by means of models reconstructed from serial sections of elder pith, has studied the form of the typical cells of one mature plant tissue. KELVIN had demonstrated mathematically in 1887 that of all bodies which may be combined to fill space without interstices a tetrakaidecahedron, or figure having 14 surfaces, certain of which are slightly curved, rivaled the rhombic dodecahedron of KIESER in inclosing "the greatest space with the least extent of surface." By actual count of the numbers of contacts which each cell of elder pith has with those surrounding it, LEWIS has determined that these cells actually are approximately 14-sided, a mean number of 13.96 contacts having resulted from counts on 100 cells. More than half are 13, 14, or 15-hedra. "Cells with an excessive number of contacts are usually large, and of such form as to suggest that an expected division in some particular plane has failed to occur." The manner of restitution of the tetrakaidecahedron following cell division, which produces an 11-sided figure, whether the bisecting plane be vertical or transverse, was determined by a study of actual cell models.—F. WEISS.

Light and growth of plants.—Ever since the work of GARNER and ALLARD, showing a close relationship between the length of day and growth and reproduction in plants, plant physiologists have felt the need of a thorough study of the chemical conditions existing in plants exposed to light for different periods of time. A recent paper by NIGHTINGALE[5] does much to supply this need. Using mainly the tomato, but including several other plants, he exposed the plants to light for different lengths of time, and also varied the amount of nitrogen in the nutrient solution. He finds that in the tomato it is the carbohydrate-insoluble nitrogen ratio, rather than the carbohydrate-total nitrogen ratio that is significant in determining the type of growth. Strongly vegetative unfruitful plants were secured under conditions resulting in a high proportion of insoluble nitrogen to carbohydrates. These conditions were a short day and a good nitrate supply. If the nitrogen supply was kept up and the day lengthened, conditions were present for the formation of an abundance of insoluble nitrogen and also of carbohydrates. The result was strongly vegetative and fruitful plants. Conditions of long day and low nitrate supply resulted in a high proportion of carbohydrate to insoluble nitrogen and a weakly vegetative and unfruitful plants. Buckwheat, soy beans, radish, and *Salvia* seemed to require a certain duration of light as well as a supply of carbohydrates for the synthesis of nitrates to insoluble nitrogen. This was not true

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[4] LEWIS, F. T., The typical shape of polyhedral cells in vegetable parenchyma and the restoration of that shape following cell division. Proc. Amer. Acad. Arts and Sci. **58**:537–552. 1923.

[5] NIGHTINGALE, G. T., Light in relation to the growth and chemical composition of some horticultural plants. Proc. Amer. Soc. Hort. Science 1922: 18–29.

in the case of the tomato, at least within the limits of the light exposure tested.—S. V. EATON.

Light penetration into seawater and plant distribution.—Using a Kunz photo-electric cell, SHELFORD and GAIL[6] have made a study of light penetration into seawater under different conditions. They find that in clear, calm weather the surface of the water shuts out 25 per cent of the sunlight. If the surface is rough, as high as 70 per cent may be shut out. When the surface of the water is smooth, about 60 per cent of the light penetrates to a depth of 1 m. The authors also studied the penetration of light of different wave lengths. Then this quantitative data is related to the distribution of vegetation. Most of the brown algae are found at a depth of 10 m., where the short waves of light are about 10 per cent and the red about 0.99 per cent of full sunlight. The red algae are found between 15 and 25 m., where the shorter wave lengths are between 10 and 2 per cent and the red between 0.99 and 0.0032 per cent of full sunlight. Thus in both cases, the energy for photosynthesis is mainly from the shorter wave lengths. The work has been done carefully and accurate quantitative data on at least one of the factors affecting plant distribution in the sea have been determined.—S. V. EATON.

Sand and water cultures.—In a series of carefully planned and conducted experiments with Marquis wheat, BAKKE and ERDMAN[7] studied the best proportions of the three salts KNO_3, $CaH_4(PO_4)_2$, and $MgSO_4$, for optimum growth in sand cultures as compared with these in water cultures. The data reported include records of transpiration, green and dry weights, temperature, evaporating power of air, radiant energy, and hours of sunshine. Pronounced changes in hydrogen ion concentration during the final 3.5 day period of growth (and hence presumably in earlier periods also) are shown to have occurred. The tendency to approach neutrality was greater in the sand than in the water cultures. No correlation could be shown between total yields and reaction values of the nutrient media, a result which might have been anticipated in the absence of buffered solutions. The water culture giving most favorable growth of top had 2/8 of its total osmotic concentration derived from KNO_3, 1/8 from $CaH_4(PO_4)_2$, and 5/8 from $MgSO_4$. With sand, best top growth was attained in a corresponding 3/8 KNO_3 solution, 3/8 $CaH_4(PO_4)_2$, and 2/8 $MgSO_4$. Transpiration and green and dry weights of tops were generally higher in the water cultures, but greatest root development occurred in the sand cultures. In general, transpiration records over the entire period of growth, and dry weight records of tops and roots, show parallel variations.—R. B. DUSTMAN.

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[6] SHELFORD, V. E., and GAIL, F. W., A study of light penetration into seawater made with the Kunz photo-electric cell, with particular reference to distribution of plants. Publ. Puget Sound Biol. Sta. **3**:141–176. 1922.

[7] BAKKE, A. L., and ERDMAN, L. W., A comparative study of sand and solution cultures of Marquis wheat. Amer. Jour. Bot. **10**:18–31. 1923.

Hydrogen ion injury.—Certain abnormalities and retardations of root development in nutrient solutions made up to contain relatively high amounts of dihydrogen phosphates have been traced by Miss ADDOMS[8] to hydrogen ion injury. She deserves credit for having employed the dark field illuminator in making the injuries visible. The injurious effects seem to be due to a coagulation of the protoplasm of the root hairs. The range studied runs from P_H 3.94 to 3.47, a rather narrow range, and it is possible that the experiments did not run long enough to show whether the least concentration of hydrogen ion used is really harmless to protoplasm. The statement that there can be no direct relation between the hydrogen ion concentration of nutrient solutions and the yield of plants grown in them may need interpretation. If it is meant that there is no correlation between hydrogen ion concentration and yield, one would want statistical data as proof. The definitions of gel, coagulation, and flocculation appended in a foot note seem to the reviewer not in accord with the common use of the terms. Some authors describe reversible gel formation in the protoplasm.—C. A. SHULL.

Availability of mineral plant food.—A modification of the generally accepted views of mineral availability is offered by COMBER.[9] In connection with the assumption that all nutrients must dissolve in soil water before absorption, certain inconsistencies are pointed out. These include the relation of the composition of the soil solution to the mineral elements absorbed and the water transpired by the plant, the absorption of iron, and the availability of phosphates. Feeding in the soil and in nutrient solutions is held to be unlike. The possibilities are suggested, first that the plant may absorb colloidal particles, and second, that there may be a union of the root hair with the soil particles, through their respective hydrophilous colloids, in such a way that the two form one system through which the dissolution of the soil particle by the organic matter of the root hair is more readily accomplished.—R. B. DUSTMAN.

Wild flowers of South Africa.—An attractive magazine[10] on much the same lines as the well known CURTIS' *Botanical Magazine* is now in its third year. It contains hand colored plates of the flowering plants indigenous to South Africa, with accompanying botanical descriptions. The illustrations are mostly from drawings by Miss K. A. LANSDELL and Miss S. GLOVER, while the descriptions have been prepared by E. PERCY PHILLIPS, botanist in charge of the National Herbarium at Pretoria. The current volume begins with plate 81, illustrating *Clematopsis Stanleyi*, a small shrub of the Ranunculaceae. The

[8] ADDOMS, RUTH M., The effect of the hydrogen ion on the protoplasm of the root hairs of wheat. Amer. Jour. Bot. **10**:211–220. 1923.

[9] COMBER, N. M., The availability of mineral plant food. Jour. Agric. Sci. **12**:363–369. 1922.

[10] The flowering plants of South Africa, edited by T. B. POLE EVANS. Quarterly. Pub. by Specialty Press of South Africa, Johannesburg and Cape Town. 60*s* annually.

quality of the illustrations seems to compare favorably with that of the publication after which it was modeled, while the remarkable diversity of the flora of South Africa affords many unique flowers to attract the attention of artists as well as botanists.—GEO. D. FULLER.

Defoliation and blossom bud formation.—ROBERTS[11] finds that defoliation has a marked inhibiting effect on the formation of flower buds. There was a close relation between the removal of fractional parts of the leaf and the number of buds formed, the more of the leaf removed the greater the inhibition. While the effect is largely localized at the node where defoliation takes place, there is some effect in reducing the number of buds formed at adjoining nodes. The length of the spurs growing at nodes defoliated the preceding season was less than in the case of spurs growing at undefoliated nodes. It is suggested that this may be due to the greater nitrogen reserve of the undefoliated nodes. It would be interesting to study further the chemistry of the defoliated and undefoliated nodal tissue. This will no doubt be done in later work. The present report is part of the preliminary work that has been done on the general problem of the formation of buds by fruit trees.—S. V. EATON.

Fungicidal action of sulphur.—Sulphur has been much used as a spray material in the control of plant diseases without our knowing in what way it exerted its toxic effects. YOUNG[12] has made a careful study of its action, and finds that the toxic compound which makes it a good fungicide is pentathionic acid, $H_2S_5O_6$. The pentathionic acid forms an excellent adsorption medium to bind together $S\mu$ and water into a hydrophilic colloidal sulphur, as represented by the formula $S_5O_6\overset{\cdot}{H_2}\overset{\cdot}{S}\overset{\cdot}{H_2}O$. This hydrophilic colloidal sulphur exhibits toxicity only at P_H 4.2–5.4, because the pentathionic acid is unstable at hydrogen ion concentrations on either side of this range. This work explains the effectiveness of various colloidal sulphur sprays which have been introduced in the last few years in Australia and Europe.—C. A. SHULL.

Lichens and glass.—Miss MELLOR[13] has recently added to her interesting contributions to our knowledge of the ability of lichens to etch the surface of glass windows. Her previous work, noted in this journal,[14] is now sup-

[11] ROBERTS, R. H., Effect of defoliation upon blossom bud formation. Wis. Agric. Exp. Sta. Res. Bull. 48. pp. 15. *figs.* 5. 1923.

[12] YOUNG, H. C., The toxic property of sulphur. Ann. Mo. Bot. Gard. **9**:403–435. 1922.

[13] MELLOR, ETHEL, Lichens and their action on the glass and leadings of church windows. Nature **112**:299–300. 1923.

[14] BOT. GAZ. **73**:423. 1922.

plemented by further evidence. Twenty-three species and varieties are recognized as frequenting this curious habitat, of which *Diploicia canescens* is most abundant.

Some of Miss MELLOR's conclusions have been called in question by HEATON,[15] who regards the decay of the glass of old stained glass as the cause of the presence of lichens, rather than the reverse. This criticism brings a reply from Miss MELLOR,[16] whose contention that lichens cause disintegration of the surface of stained glass and the production of pits seems to be well supported by her evidence.—GEO. D. FULLER.

Vegetation of Himalayas and of Corsica.—The first[17] of two recent numbers of the Vegetationsbilder contains excellent illustrations of monsoon forest, *Quercus incana* forest, *Pinus longifolia* forest, and of *Euphorbia Royleana* scrub, all from the slopes of the western Himalayas.

The second number[18] is devoted to the vegetation of Corsica, and gives illustrations of *Nerium oleander*, *Arundo donax*, *Gomphocarpus fruticosus*, and *Helleborus trifolius*, together with photographs of macchie, forests of *Pinus nigra*, *Abies alba*, and of *Fagus silvatica*.—GEO. D. FULLER.

Sexual state of plants.—SCHAFFNER,[19] in continuation of his investigation of sexuality, has published results of work with *Acnida tamariscina*, *Thalictrum dasycarpum*, *Acer saccharinum*, *A. rubrum*, *Thalictrum dioicum*, and *Aesculus glabra*. He is convinced that the various expressions of sexuality can be arranged in "a progressive series of many stages in respect to the intensity and fixity of the sexual state, all depending on a fundamentally similar physiological activity." He gives a sequence of eight of the more prominent stages, beginning with typical bisporangiate species, and through intermediate stages culminating in dioecious species with no intermediates and no sex reversal.—J. M. C.

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[15] HEATON, N., Lichens and their action on the glass and leadings of church windows. Nature, 505–506. 1923.

[16] MELLOR, ETHEL, Lichens and their action on the glass and leadings of church windows. Ibid. 506. 1923.

[17] KENOYER, L. A., Waldformationen des westlichen Himalaya. Vegetationsbilder, Karsten and Schenck **15**: heft 1. *pls. 1–6*. 1923.

[18] RIKLI, M., and RUBEL, E., Korsika. Vegetationsbilder, Karsten and Schenck **15**: heft 1. *pls. 7–12*. 1923.

[19] SCHAFFNER, J. H., Observations on the sexual state of various plants. Ohio Jour. Sci. **23**: 149–159. 1923.